Ecological Resilience at Semi-arid and Temperate Boundaries of the Mediterranean-type Fynbos Biome, South Africa, during the Holocene

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ABSTRACT

Mediterranean-type ecosystems are amongst the most vulnerable to global change. Threats from desertification are projected due to rapid expansion of adjacent semi-arid systems. Changes in fire frequency and intensity can alter ecosystem composition and structure, and potentially facilitate transitions between alternative stable states. Given the outstanding biodiversity of the Mediterranean-type fynbos biome in the Greater Cape Floristic Region (GCFR) of South Africa, understanding of the long-term impacts of global change are particularly important. In this study, palaeoecological data are used to assess the effects of changes in climate, fire and land use on vegetation at the semi-arid and temperate margins of the fynbos biome.

Previous palaeoecological studies have shown stable fynbos during the recent geologic past, which restricts interpretation of the long-term ecological processes that determine biome resilience. This study sourced sediment cores directly from present-day fynbos-succulent karoo (semi-arid) and fynbos-afrotemperate forest biome boundaries to emphasise ecological dynamics. Fossil pollen, spores and charcoal were extracted from radiocarbon dated sediment cores to provide proxies for vegetation, hydrology, large herbivore abundance and fire. Constrained hierarchical clustering (CONISS) and Non-metric Multidimensional Scaling (NMDS) was applied to the fossil data to identify distinct assemblages in the record, and to further elucidate ecosystem trajectories through time.

At the semi-arid boundary (5,500 cal yrs BP - near present), decreased moisture and fire from 4,000-735 cal yrs BP allowed colonisation of fynbos by a possible 'no-analogue' community dominated by Asteraceae and Poaceae. From 735 cal yrs BP however, climatic amelioration allowed fynbos to re-establish and the system can therefore be viewed as resilient through a capacity for 'recovery' and persistence through turnover in internal composition of fynbos taxa. This sensitive response to climatic forcing reflects the dominant influence of physiological stress at the semi-arid limits of Mediterranean-type ecosystems, as well as a Gleasonian type community composition with loose species associations. In contrast, ecosystem

dynamics at the temperate boundary were dominated by internal feedback processes that promoted remarkable between-biome stability, and the persistence of distinct biomes with strong internal organisation. Further, a phylogenetic perspective suggests the high fluidity of the fynbos-succulent karoo ecocline relative to the fynbos-afrotemperate forest ecotone reflects comparative evolutionary histories of the respective biomes. At the within-biome scale, both sites manifest impacts of pastoralism during the past 1,500 years which, through interactions among herbivory, fire, and climate, promoted persistent alternative stable states within fynbos. The degraded states were characterised by decreased functional diversity and the dominance of a palaeo-invasive plant species.

This thesis makes a significant contribution to the understanding of fynbos resilience by explicitly investigating the expression of resilience through resistance and recovery. Moreover, the relevance of the findings have been amplified by framing the study within a bioclimatic and theoretical framework that is relevant to contemporary and future environmental and ecological change in the GCFR. By identifying when, where and why abiotic, biotic and disturbance parameters become more/ less significant provides important fundamental information regarding how this and other Mediterranean-type biomes might respond to potential future change scenarios.

Keywords: Palaeoecology, global change, alternative stable states, resistance, recovery, succulent karoo, afrotemperate forest, Cape Flora.

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1. INTRODUCTION

Global changes in climate and land use are causing substantial changes in the distribution, structure and function of the Earth's biota (Estes, et al. 2011; Parmesan, et al. 2011). Ecological systems may be subject to rapid, catastrophic shifts as their capacity to tolerate climate and land-use change is eroded and critical thresholds are reached (Scheffer, et al. 2001). This is particularly pertinent in Mediterranean-type ecosystems that are highly sensitive to these changes and harbour an outstanding proportion of the word's biodiversity (Keeley, et al. 2012). The Greater Cape Floristic Region of South Africa has a higher species concentration per unit area than any of an equivalent size on the planet, and is currently threatened by climate and land-use change (Allsopp, et al. 2014). This thesis explores the possibility that biomes in this region will change in structure, function and distribution by investigating past ecological changes evidenced in the Holocene palaeoecological record. The study is framed by the themes of alternative stable states and resilience theory (Holling, 1973; Holling, et al. 2002; Oliver, et al. 2015; Scheffer, et al. 2001). Further, it addresses fundamental debates regarding global biogeography, including the significance of abiotic, biotic and disturbance drivers and their interactions in promoting biome dynamics and conservatism (Crisp, et al. 2009; Darwin, 1859; Louthan, et al. 2015; MacArthur, 1972; Potts, et al. 2015; Verboom, et al. 2014; Schimper, 1903; Slingsby, et al. 2014). By examining vegetation dynamics at semi-arid and temperate boundaries of the fynbos biome, an evaluation of the significance of biotic, abiotic and disturbance factors - as well as life-history and plant-functional traits - can be made.

1.1. THE FYNBOS BIOME AND GLOBAL CHANGE IN CONTEXT

Mediterranean-type ecosystems provide exemplary natural laboratories to study global change. They are highly sensitive to climatic and land-use changes, as well as interactions among these and associated drivers (Doblas-Miranda, et al. 2015; Keeley, et al. 2012). Located between around 30 and 40 degrees latitude (north and south) on the southern and western continental margins of the Europe, North America, South America, Australia and Africa (Figure 1.1), these regions are highly sensitive to

global atmospheric change because they are transitional in nature between semi-arid and temperate climates (Ackerly, et al. 2014). Fire is an essential component of these systems, and is strongly tied to climate through the effect of the latter on fire fuel, conditions and ignition, as well as controlling the distribution of many fire-sensitive and dependent plant taxa. The evolution of fynbos is intricately linked to both Mediterranean-type climate and wild fire, which emerged in response to the development of the Benguela Upwelling System at least around 10 million years ago (Verboom, et al. 2009; Verboom, et al. 2014). These systems harbour some 20 % of global vascular plant diversity in only 2 % of total land area (Cowling, et al. 1996; West, et al. 2012).

The global distribution of the fynbos biome is restricted to the south west of South Africa (Figure 1.1). It is a megadiverse, sclerophyllous, fire-prone shrubland (Allsopp, et al. 2014; Cowling 1995). Harbouring around 8,600 species in an area of 90,000 km2, fynbos holds a greater species density than any area of equivalent size on Earth (Cowling, 1995). Disconcertingly, 1,736 of these species feature on the Red Data list as 'in danger of extinction' (Raimondo, et al. 2009). Furthermore, it has been predicted that climate change might drastically reduce the present bioclimatic envelope of fynbos; however more localised re-shuffling of species could also occur, the forecast depending on the modelling approach used (Altweg, et al. 2014). Predictions of how land use and fire will interact with climate change are less certain still (Kraaij, et al. 2014) and is likely to be further complicated by invasive species. Greater understanding of the factors governing fynbos structure, function and distribution at its biogeographical, climatic and ecological limits is therefore required to develop adaptive strategies in the face of present and future global change (Slingsby, 2014).

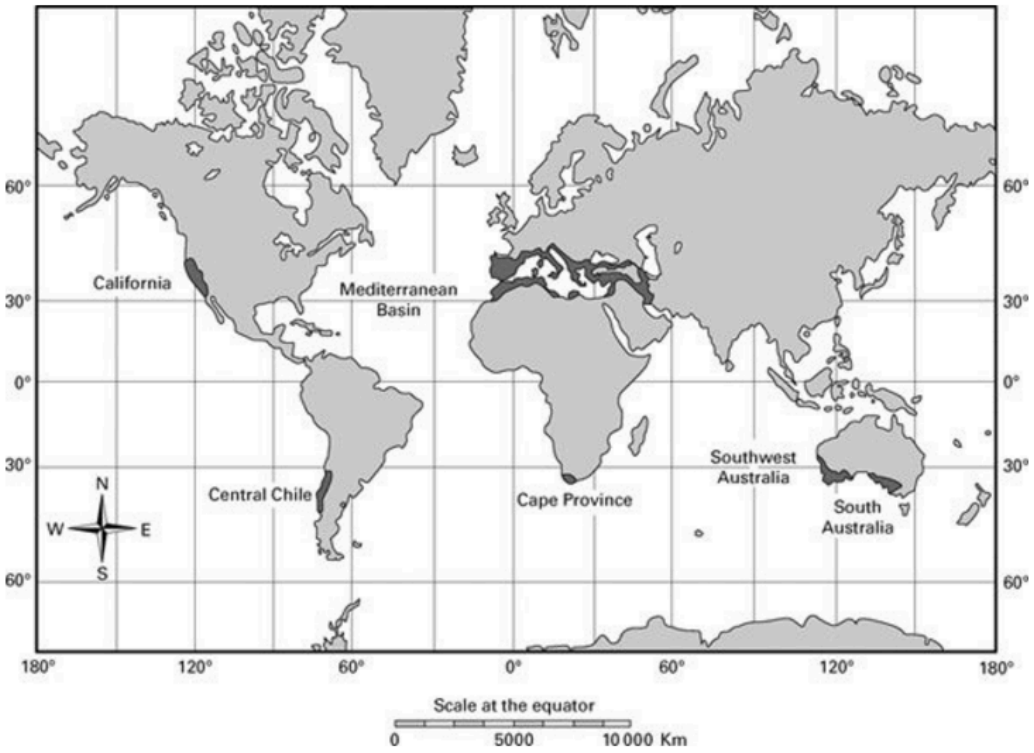

Figure 1.1. Mediterranean ecoregions of the world. Figure from Keeley, et al. 2012.

Fynbos is considered a Mediterranean-type biome due to the physiognomy and functional ecology of its flora, as well as being associated with a winter rainfall and hot, dry summers climate (Ackerly, 2014). It is characterised by predominance of screlophyll shrubs and the prevalence of fire, the latter being fundamental to biodiversity and ecological process within all Mediterranean-type ecosystems, and its key floristic sub-types are characterised by the familial dominance of either Proteaceae, Ericaceae, Restionaceae, Asteraceae or Poaceae (Keeley, et al. 2012). True Mediterranean climate occurs only in the extreme south west around Cape Town, where mild, wet winters and hot dry summers dominate due to seasonal shifts between the winter-rain bearing temperate westerlies and the dry sub-tropical anticyclone. Northwards from this Mediterranean climate zone along the western flank of South Africa, rainfall amount, biomass production and fire prevalence decrease as the climate transitions to semi-arid (Figure 1.2). This semi-arid region is dominated by the succulent karoo, a shrubland dominated by dwarf leaf-succulents, in particular of Aizoaceae, Euphorbiaceae and Crassulaceae, as well as annuals of Asteraceae (Desmet, 2007; Cowling, et al. 1999). In contrast to fynbos, succulent

karoo is not fire prone nor adapted, and is much more tolerant of aridity. Therefore at this low latitude margin, it is expected that climate will dominate fynbos dynamics due to the increasing aridity gradient. This may occur both directly by limiting fynbos growth and persistence, but also indirectly by reducing fire prevalence through limitation of biomass production and ignition.

Along the south east coast of the fynbos biome summer rainfall increases, resulting in more aseasonal climate with year-round rainfall. The Tsitsikama region east of George (Figure 1.2) contains the only substantial representation of afrotemperate forests, which are extremely rare in South Africa. Structurally, these are tall, multilayered temperate rainforests dominated by yellowwoods (*Podocarpus* and *Afrocarpus*) (Bergh, et al. 2014; Geldenhuys 1991). Most are set amongst fynbos archipelagos reflecting a relict distribution of ancient forests that dominated the region until around 10 million years ago when fynbos proliferated (Mucina and Rutherford, 2006; Verboom, et al. 2014). Afrotemperate forests are fire intolerant, and mainly occur in topographic fire refugia, though they also can expand into fynbos when fire is suppressed (Slingsby, et al. 2014). Both vegetation types can co-exist within the same climate space, and can establish and persist on the same geologic substrate. Fire is thus suggested as key in determining the relative distribution of fynbos and afrotemperate forest. While climate and fire are expected to be strongly interlinked at this biome boundary, it is also expected that vegetation itself will act to promote and/ or depress fire as reduced physiological stress facilitates stronger biotic control than at the semi-arid boundary.

These north-south and east-west bioclimatic gradients define the Greater Cape Floristic Region (GCFR), which comprises fynbos, succulent karoo, renosterveld, subtropical ticket and forest biomes (Bergh, et al. 2014) (Figure 1.2).

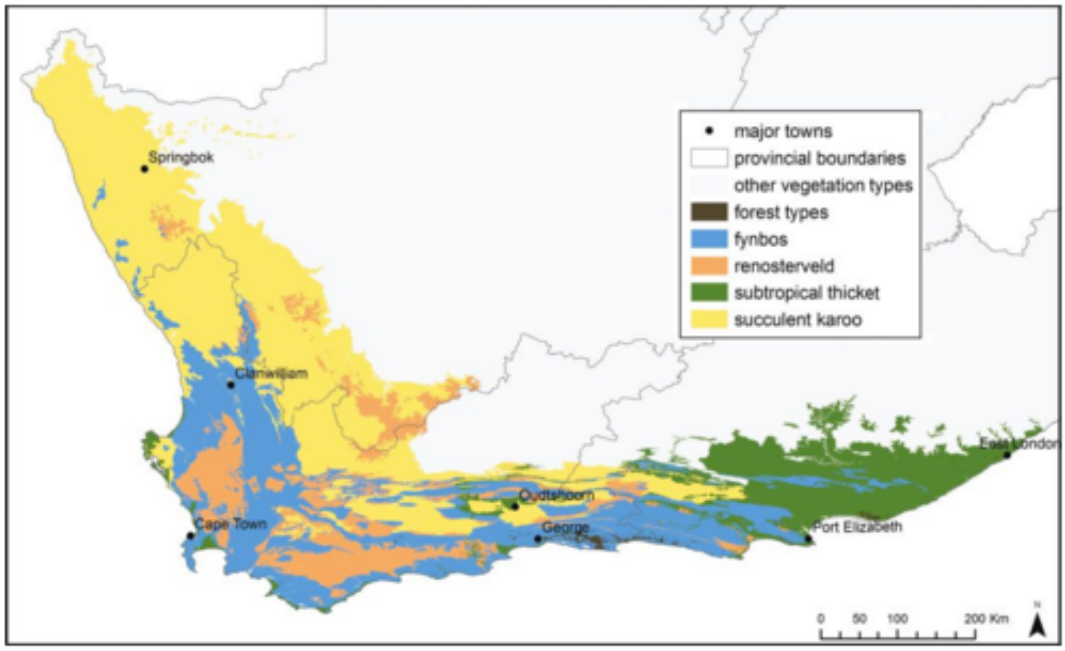

Figure 1.2. Biomes of the Greater Cape Floristic Region. Figure from Bergh, et al. (2014).

Climate data from the last century show that the GCFR has become significantly warmer (Haensler, et al. 2010; Hoffman, et al. 2011; Hoffman, et al. 2009; Midgley, et al. 2005; New, et al. 2006). This trend is very likely to continue and climate in the GCFR could be 1-3^{o}C warmer by 2100 (Engelbrecht, et al. 2009; Hewitson and Crane, 2006; Tadross, et al. 2005). Rainfall trends are more spatially complex. Winter rainfall will likely be reduced leading those areas in the heart of the current winter rainfall zone (WRZ) to become drier overall. Areas associated with the year-round rainfall zone (YRZ) toward the east of the region are also likely to see decreases in winter rainfall, though this may be offset by increases in summer rainfall as the present summer rainfall zone (SRZ) is expected to become wetter (Altweg, et al 2014; Engelbrecht, et al. 2009; Hewiston and Crane, 2006; MacKellar, et al. 2007).

Bioclimatic biome envelope modelling suggests a substantial contraction of preset fynbos climate space, and poleward expansion of that associated with succulent karoo, which might lead to substantial species losses (Bomhard, et al. 2005; Hannah, et al. 2005; Midgley, et al. 2002, 2003; Rutherford, 2000). Increased aridity and associated reductions in fire prevalence might lead fynbos to be invaded by drought-tolerant, fire-sensitive succulent karoo species (Wilson, et al. 2015). In contrast,

projections employing bioclimatic species niche approaches suggest that more localised shifts and reshufflings of species will occur (Driver, et al. 2012), requiring understanding of local rather than regional processes (Gillson, et al. 2013).

Where moisture availability is not limiting to biomass production in fynbos, such as in regions where afrotemperate forest occur, fire frequency and intensity are anticipated to increase as a result of hotter temperatures and increased incidence of summer drought (Wilson, et al. 2010; Southey, 2009). This scenario is complicated, however, as fire regimes result from interaction among climate, vegetation and land use, that latter of which is distinctly heterogeneous and can both promote or suppress fire. Afrotemperate forest taxa are excluded from fynbos habitat by frequent fire (Geldenhuys, 1994), therefore forests can only expand into fynbos where fire is suppressed by land use and/or natural topography. In Table Mountain National Park afrotemperate forest cover has increased by over 65 % since c. 1945 (Poulsen and Hoffman, 2015; Poulsen 2013). This has led to concerns over invasion of fynbos by forests to the detriment of biodiversity, but the trend may also reflect a recovery from historic forest clearance (Luger and Moll, 1993).

Previous palaeoecological studies in the fynbos biome (Meadows and Sugden, 1991, 1993; Meadows, et al. 2010; Valsecchi, et al. 2013; Quick, et al. 2011, 2015) have suggested that fynbos has a high capacity for resilience, which is maintained by internal adaptation through overturning among fynbos sub-types with varied capacities for resistance to climate and fire (e.g. mesic, frequent-fire loving ericaceous fynbos verses drought-tolerant, slower maturing proteoid fynbos) (Valsecchi, et al. 2013). Research on drought resistance in fynbos (Agenbag, et al. 2007; Mustart, et al. 2012; West, et al. 2012) has yielded three main findings; 1) responses to drought are highly variable among co-occurring species; 2) mature woody plants are highly resistant to drought; and 3) seasonality of drought is the primary factor determining drought response (Altweg, 2014). Interactions among climate and fire are particularly important, pre- and post-fire conditions being sensitive to ecological processes owing to the high diversity of functional traits and the centrality of fire in the biome's ecology (Keeley, et al. 2012). Land-use changes may interact with fire and climate and modify their effects. For example clearing and burning of forest was prevalent in

the 19th century whereas fire suppression and forest regrowth has been observed in the 20th century (Poulsen, 2013). The extent to which present fynbos-forest distributions are a product anthropogenic land-use and management practices in the historical and archaeological periods is however poorly resolved, but can be elucidated using palaeoecological records.

At present in the fynbos biome, one of the greatest threats to biodiversity is posed by invasive species (Slingsby, et al. 2014; Wilson, et al. 2014; Kraaij, et al. 2014). Invaders can be seen to promote shifts to undesirable alternative stable states (Holling, 1973; Lewontin 1969; Scheffer, et al. 2001), which often occur as a result of interactions among climate, fire and land-use change with so called 'biotic modifiers', or 'ecosystem engineers' (Linder, et al. 2012). These taxa fundamentally alter the abiotic and biotic environment and modify ecological filtering processes, which often results in the persistence of (undesirable) alternative stable states (Slingsby, et al. 2014). Some of the most prolific and well known contemporary ecosystem engineers are invasive alien species (e.g. *Pinus pinaster, Acacia mearnsii*) (Wilson, et al. 2014). Indigenous species too can act as biotic modifiers and, often associated with a change in land use (Slingsby, et al. 2014), can be protagonists in the development of undesirable and persistent alternative stable states (Gillson, et al., 2008). By studying past invasions through the lens of palaeoecology, greater understanding of the processes of invasion can be gained by making ecological observations before, during and after invasions, and against a backdrop of long-term environmental change relevant to the future.

1.2. FYNBOS DYNAMICS AND RESILIENCE TO GLOBAL CHANGE

Biomes were first defined as globally convergent plant structural formations along with the ecosystems and biogeochemical cycles they support (Holdridge, 1947; Schimper, 1903; von Humboldt, 1807). Climate is central to the biome concept, but it is also widely acknowledged that more than one biome type can exist within the same climate space, and that disturbance, biotic interactions and edaphic factors can all play a role in determining biome boundaries (Moncrieff, et al. 2015; Slingsby, et al. 2014; Whittaker, 1975). Ecological processes such as competition for resources, and

disturbances including fire and herbivory, may be deterministic in biome organisation and extent (Bond, et al. 2005a, b, c; Burger and Bond, 2015; Coetsee, et al. 2015; Coetsee, et al. 2013; Hoffmann, et al. 2012). In regions of scarce resources, such as deserts, biota are often dominated by abiotic stress. Where moisture resources are in superfluous supply and temperature is not limiting, such as in temperate climate regions, biotic interactions and disturbance may be more significant in biome dynamics (Brown 1995; Darwin, 1859; Dobzhansky 1950; Louthan, et al. 2016; MacArthur 1972; Merriam, 1894; Schimper, 1903; Walter, 1971; von Humboldt, 1807). There may therefore be a general tendency for semi-arid boundaries of Mediterranean-type biomes such as fynbos to be more strongly defined by climate than are temperate boundaries.

This situation is however highly complex for a number of reasons. Firstly, biomes and the functioning of their ecosystems are to varying extents a product of abiotic, biotic and disturbance parameters their complex interactions (Slingsby, et al. 2014; Wessels, et al. 2011). Moreover, the global distribution of physiological stressors is highly heterogeneous (Seddon, et al. 2016). In order to understand the impacts of global change on Earth's biota, it is therefore a priority to understand when, where and why abiotic and biotic process, as well as their interactions, determine biome distributions. One approach to untangling this is to compare dynamics at low (semi-arid) and high (temperate) latitude edges of (Mediterranean) biomes.

Understanding of global change is framed well by the concept of resilience, and this is particularly appropriate to the study of biome boundaries which represent thresholds in some combination of biological and environmental parameters. This emphasises that ecosystems (*sensu* biomes) have variable capacities to maintain their fundamental nature (Holling, et al 2002; Holling, 1973). Ecosystems can be resilient by either resisting changes in response to perturbations, or by recovering their original character following a change (Hodgson, et al. 2015; Oliver, et al. 2015). If the resilience of an ecosystem is exceeded, it may reorganise into one of multiple possible alternative states, each with its own fundamental properties and associated resilience mechanisms (Holling 1973; Beisner, et al. 2003). Alternative stable states theory is suited to this study as it stresses both intrinsic biotic processes (Drake 1991; Lewontin

1969) and changes in abiotic parameters (May 1977, Scheffer et al 2001), while also facilitating understanding of interactions between these two spheres (Beisner et al 2003; Vetter 2009). Such phenomena are documented worldwide from local to global scales in a variety of systems, though it is yet to be understood how persistent these transformed states are (Dakos, et al. 2015; Petraitis, et al. 2013; Schröder). In the face of global change, and with a desire to maintain ecosystem functions, biodiversity and the associated services these bring to society (Oliver, et al. 2015), it is crucial to identify where abiotic and biotic factors determine the potential for alternative ecosystem states, and what factors might trigger state shifts (Slingsby, et al. 2014).

In the Greater Cape Florist Region, multiple abiotic and biotic factors combine to create complex environmental filters determining relative biome distributions (Slingsby, et al. 2014; Cowling, et al. 2014). Prior to the Late-Miocene, afrotemperate forest (and thicket) were a consistent and prominent component of the GCFR, and are the oldest component of the flora dating from at least the Palaeogene ~70 Ma. However, aridification towards the end of the Miocene, in concert with the establishment of prevalent, recurrent wildfires, likely drove a rapid decline in the abundance of forest elements and replacement with arid- and fire-adapted floras (DuPont, et al 2011). Succulent karoo evolved substantially later than did fynbos (Verboom, et al. 2009), apparently in response to the regional development of strongly a seasonal winter rainfall climate driven by intensification of the Benguela Upwelling System around 3-5 Ma (Verboom, et al. 2014). The present ecology and distributions of the GCFR flora attests to these comparative life histories.

At its semi-arid distribution limits, fynbos expansion into succulent karoo appears to be inhibited by the relatively low tolerance of aridity stress of fynbos taxa. Conversely, succulent karoo taxa are excluded from fynbos habitat by fire and competition as fynbos species have higher growth rates (Carrick 2001, 2003; Esler, et al. 2015; Jacobsen et al 2009; Lechmere-Oertel and Cowling, 2001). Only in the absence of fire might competition between fynbos and succulent karoo species become deterministic (Rebelo, et al. 2006; Wilson, et al. 2015).

At its temperate distributional limit, fynbos and afrotemperate forest are capable of living in very similar abiotic environmental conditions, surviving within the same climate and on the same geological substrate (Manders and Richardson, 1992). Fynbos is excluded from forest on the basis that shade is high and fire uncommon in forest environments, and abundant light and fire are required for fynbos growth and reproduction (Slingsby, et al. 2014). Forests species can only expand into fynbos and persist where fire is excluded from fynbos by land use and natural topography, and aridity stress is not limiting (Geldenhuys, 1994; Luger and Moll, 1993). This exclusion must be of significant duration to allow forest pioneers to attain fire resistant traits and subsequently facilitate establishment of secondary forest taxa that might shade-out fire-prone fynbos (Coetsee, et al. 2015, 2013; Hoffmann, et al. 2012). Therefore there exists a range of processes determining biome distribution at this biome boundary, ranging from strongly abiotic in semi-arid habitat, to strongly biotic consumer control where aridity is less severe. At this relatively mesic biome boundary therefore, biotic factors tend to dominate.

Biomes are said to be major selective biological filters (Crisp, et al. 2009). Their constituents tend to have shared evolutionary histories, which leads to the possession of similar life-history traits and results in alteration of the abiotic and biotic environment and niche construction (Linder, et al. 2012). This in turn modifies environmental filtering processes and restricts species immigration (Slingsby, et al. 2014). Upon arrival in a recipient community, an immigrant species is confronted with the challenges of a new environment (Potts, et al. 2015). Some level of pre-adaptation is obviously advantageous, therefore lineages derived from areas where conditions similar to the destination environment prevail are clearly at an advantage (Verboom, et al. 2014). It should therefore be expected that ecosystem resistance to colonisation is much higher at between- verses within biome scales. Palaeoecology offers the potential to investigate past colonisations (‘palaeo-invasions’; Gillson, 2008; Gillson, 2009), and so elucidate the long-term processes and interactions governing the process on timescales of decades to millennia. Understanding of these interactions over centennial – millennial timescales here will provide a deeper understanding of long-term patterns of invasive spread (Froyd and Willis, 2008).

Biome boundaries are particularly valuable in identifying global change impacts. Being transitional areas between biotic community distribution limits, they are sensitive to environmental change and provide a microcosm to observe the interactions between biotic and abiotic processes (Altweg, et al. 2014; Cumming, 2011; Holland, et al. 1991; Hobbs, 1986; Potts, et al. 2015; Whittaker, 1960; van Leeuwen, 1966). Gradual transitions are often controlled to some progressive change in an abiotic gradient (Curtis 1959; Gleason, 1939; Whittaker 1975) whereas zones of rapid species turnover may be indicative of ecological communities that are highly structured, discrete entities, with strong internal feedback processes akin to homeostasis (Connell and Ghedini, 2015; Collins, et al. 1992; Clements, 1936). Sharp boundaries can also result from non-gradational abiotic controls such as stark substrate contrasts. Indeed, over much of the fynbos biome the fynbos-succulent karoo ecotone occurs rapidly, but this rather reflects a modification of the climate gradient by soil texture and associated moisture availability (Esler, et al 2015). In the Kamiesberg Mountains, Namaqualand, the fynbos-succulent karoo boundary occurs in the absence of stark substrate contrasts. It therefore provides an opportunity to observe the effects of climate, fire and herbivory without the complicating factor of soils modifying the effects of climate on moisture availability. The fynbos–afrotemperate forest boundary is by contrast very sharp, owing to high flammability and fire adaptation in fynbos and fire intolerance in forest, and occurs independent of differences in climate. Biotic drivers are therefore likely to be strong at this biome boundary.

The magnitude of the potential threat of climate change to biodiversity loss in the fynbos biome is dependent on the proximity of present and future ecophysiological and ecological thresholds. Therefore a temporal perspective is needed which provides insight into how dynamic or resilient ecotones are to different combinations of environmental and anthropogenic factors. Previous palaeoecological analyses have indicated that fynbos has been highly resilient through the present Holocene interglacial at both at its semi-arid (Valsecchi, et al. 2013; Quick, et al. 2011) and temperate margins (Quick, et al. 2015). The biome is typically characterised in fossil pollen records by overturning within fynbos in response to climatic change, while the biome as a whole persists despite this internal turnover (Meadows and Sugden, 1991,

1993; Meadows, et al. 2010; Quick, et al. 2013). The resilience of Cederberg mountain fynbos since the last glacial maximum, for example, has been attributed to a climatic buffering effect associated with orographic rainfall, and strong substrate association of fynbos and succulent karoo (Meadows et al 2010; Quick, et al. 2011; Valsecchi, et al. 2013). However, there is also a taxonomic resolution issue, whereby low fossil pollen taxonomic resolution may mask overturning of functional types within taxa, masking dynamism. Such apparent stability impedes understanding of the mechanisms underlying resilience and the nature of controls on biome distribution. It is yet to be determined whether fynbos diversity reflects resilience to climatic variability, the accumulation of species over millions of years within a climatically buffered region, or a combination of these two factors (Altweg, et al. 2014; Verboom, et al. 2009).

1.3. AIMS AND OBJECTIVES

The central aim of this thesis is to assess the resilience of fynbos to changes in climate, fire and land use at its semi-arid and temperate distribution limits.

In light of this, the following aims are identified:

- Reconstruct vegetation change at temperate and semi-arid boundaries of the fynbos biome in the palaeoecological record.
    - Assess how climate change has impacted on fynbos at its boundaries with afrotemperate forest/ succulent karoo in the past.
    - Reconstruct how fire has affected fynbos at its succulent karoo/ and afrotemperate forest boundaries in the past.
    - Infer the effects of past land-use changes on fynbos at its afrotemperate forest/ succulent karoo boundaries in the past.
    - Identify interactions among climate, fire and land use at the succulent karoo/ and afrotemperate forest boundaries in the past.

- Identify the resilience characteristics at boundaries of the fynbos biome in the palaeoecological record.
    - What are the characteristics of the temperate and semi-arid boundaries of the fynbos biome in relation to abiotic, biotic and disturbance parameters and biome organisation?
    - When/ where are biomes more/ less cohesive units/ transient assemblages?
    - Does fynbos at its boundary succulent karoo/ afrotemperate forest manifest resilience and, if so, is this through resistance and/ or recovery?
    - Are transitions between alternative stable states evident at the fynbos-succulent karoo and fynbos-afrotemperate forest boundaries in the past?
    - What can be learned by comparing resilience characteristics at the between- and within-biome scales?

In order to achieve these aims, the following objectives are defined:

- Quantify fossil pollen from sediment records located at (a) fynbos-succulent karoo and (b) fynbos-afrotemperate forest biome boundaries, allowing reconstruction of vegetation change through time.
- Reconstruct changes in fire through time using sedimentary micro- and macrocharcoal deposits
- Reconstruct herbivore abundance through time using sedimentary fungal spores
- Date sediment record using AMS ^{14}C and establish high-resolution calendar-year age models to enhance temporal perspectives on ecological processes
- Compare the records generated with published palaeoenvironmental, archaeological and historical data to aid interpretation of climate and human influence on biome dynamics.
- Quantitatively identify phases in the pollen record using pollen diagram zonation and multivariate ordination. This will allow identification of periods of relative stability and change to assess ecosystem resilience through time.

- Explore links between herbivore abundance, fire and ecosystem dynamics at the respective biome boundaries.
- Assess evidence of alternative stable states within- and between-biomes.
- Evaluate and compare the dynamics of the semi-arid (fynbos-succulent karoo) and temperate (fynbos-afrotemperate forest) biome boundaries to assess their resilience to environmental change.
- Evaluate the significance of abiotic and biotic parameters and their interactions as determinants of biome organisation in relation to global environmental change.

Through addressing these aims and objectives this thesis will contribute significantly to understanding of fynbos resilience to environmental change, fire and land-use specifically the impact of herbivory. Further, it will contribute to understanding of the resilience of Mediterranean-type ecosystems, the potential for rapid ecosystem state shifts, and the role of abiotic and biotic change in Mediterranean-type ecosystems at their temperate and semi-arid margins.

1.4. THESIS STRUCTURE

The context of the study is first set by summarising the state of current knowledge of fynbos ecology, dynamics and history in relevant areas of ecology and palaeoenvironmental research (Chapter 2). The theoretical topics covered include 'Biomes and their Boundaries', 'Ecological Resilience and Alternative Stable States' and 'Ecological Dynamics in the Palaeoecological Record'. Literature relating to the fynbos, succulent karoo and afrotemperate forest biomes, their distributions, structure and function, is then reviewed. Lastly, literature describing palaeoenvironmental change and associated palaeoecological studies are examined. The following chapter (Chapter 3) first provides detailed information on the regional study area and the sites specifically. The information presented includes relevant details of climate, vegetation, geology and land use. Secondly, Chapter 3 describes the methods used in this study, including sediment analysis, dating and age modelling; pollen, spore and charcoal extraction and analysis; data handling and statistical analyses.

Chapter 4 presents the results of the fynbos-succulent karoo boundary study, and subsequently discusses the findings in the context of the regional palaeoenvironmental record and the key ecological themes explored in this thesis. Particular attention is given to making palaeoenvironmental interpretations independent of the pollen data through use of non-pollen palynomorph indicators and sedimentology in relation to previous published analyses. The resulting reconstructions are then used as frameworks to interpret the pollen data and address the aims set out above (see section 1.2). This is similarly carried out for the fynbos-afrotemperate forest boundary in Chapter 5, though within-biome dynamics are discussed first, and between-biome dynamics of afrotemperate forest and fynbos is then discussed as evidence presented from both sites. Finally, Chapter 6 synthesises and summarises the findings of the study with particular reference to the aims (section 1.2) and compares and contrast the mechanisms of resilience at semi-arid and temperate boundaries.

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2. LITERATURE REVIEW

2.1. BIOMES AND THEIR BOUNDARIES

Biomes are the most basic unit of description and classification for the Earth's vegetation and the biota and biogeochemical cycles it supports (Olson, et al. 2001). They are defined by globally convergent plant formations with similar structural and functional properties rather than by their floristic or species composition (Moncrieff, et al. 2016). Biomes have traditionally been viewed as being in equilibrium the abiotic environment, in particular climate and soils. von Humboldt (1807) noted the occurrence of analogous vegetation formations in geographically dislocated regions with similar climatic regimes. Schimper (1903) was first to define and name the world's biomes in a way that resembles those of modern classification. He connected the dominant physiognomies of major plant formations with functional properties selected by regional climate, which implied equilibrium with climate. Later, Holdridge (1947) proposed that formations could be mapped dependent on axis of precipitation, temperature and evapotranspiration, and took this approach further by allowing modifications for soil and topography. Whittaker (1975) similarly proposed the distribution of Earth's major biomes as a function of mean annual temperature and mean annual precipitation (Figure 2.1). The latter system raises some intriguing ambiguities in predictive ability, suggesting that biome type is a function of more than temperature and rainfall alone.

Within a certain range of rainfall and temperature combinations, it is widely held that the dominant biome cannot be reliably predicted (Figure 2.1) (Bond, et al 2005a, b; 2005; Whittaker, 1975). This results from the tendency of vegetation itself to influence the environment (Moncrieff, et al. 2016). Plants and formations can alter ecological variables including climatic phenomena such as wind, temperature and moisture availability (Hoffmann, et al. 2012), soil characteristics including both texture and nutrients (Coetsee, et al. 2015; Coetsee, et al. 2013), the availability and distribution of light, and the prevalence and natural disturbances such as herbivory and wildfire (Burger and Bond, 2015; Keeley, et al. 2011; Bond, et al. 2005a, b, c). The latter is particularly pertinent in South Africa, where multiple fire-prone and fire-

intolerant biomes occur (Mucina and Rutherford, 2006). These feedbacks create the potential for multiple possible biome states where there is little significant difference in prevailing climate and underlying geological substrate. Such states can be profoundly different in terms of biodiversity and ecosystem function (Moncrieff, et al. 2016).

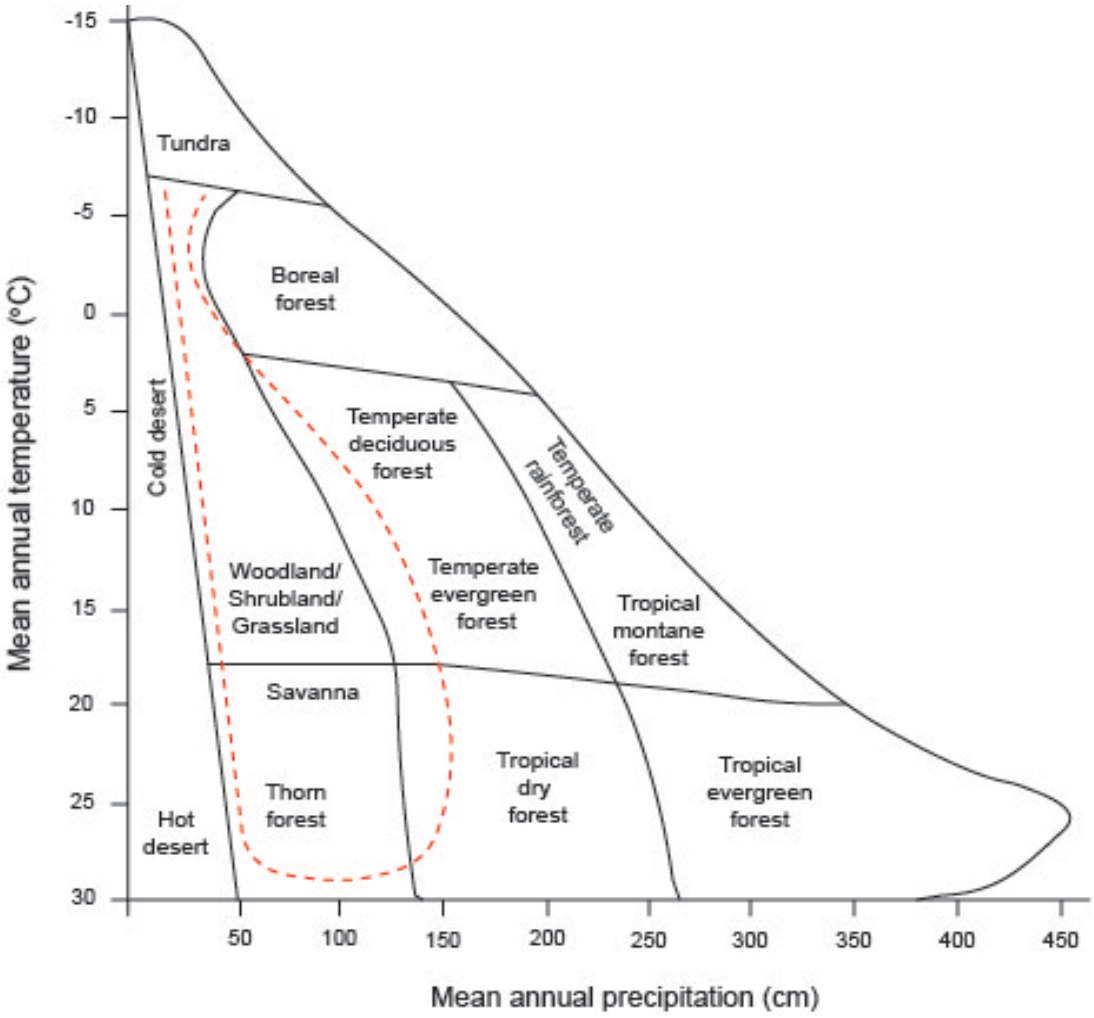

Figure 2.1. Whittaker's biome-climate ordination. Whittaker (1975) proposed that biome distributions could be predicted by precipitation and temperature. However he acknowledged within a certain climate space, climate is not a reliable predictor of biome type (red dashed line).

In studying global-scale vegetation dynamics it is important to understand fundamental constraints on plant species distributions. Most early work on geographical range limits have promoted the role of abiotic stress (Merriam, 1894; Schimper, 1903; von Humboldt, 1807). Darwin (1859) first proposed in On the Origin of Species that physiological stress determines species rages in abiotically stressful

environments. Contrastingly, in areas where abiotic resources are more abundant, he suggested that biotic interactions play a predominant role in distributions. Dobzhansky (1950), MacArthur (1972) and Brown (1995) elaborate on this, suggesting that, at high latitude distribution limits, abiotic stress determines species range shifts, while at low-latitude distribution limits biotic interactions become more important. Despite these seminal recognitions of the importance of biotic interactions in vegetation distributions, modern perspectives continue to assume that climate is the dominant determining parameter of distributions, be it directly or indirectly (Louthan, et al. 2016). Determining how modern species range shifts might change in the future is dependent on understanding when, where and why climate, biotic interactions, and disturbance become deterministic (Parmesan and Yohe, 2003). Perhaps more intriguingly, when do such factors interact to drive ecosystem dynamics?

Two general models have been proposed to explain plant species distributions in space and time. Clements' (1936) community unit hypothesis argued that plant communities are highly structured, discrete entities where termination of one group coincides with the beginning of another. This hypothesis is commonly explained schematically as a series of species abundance distribution curves that do not overlap along an arbitrary environmental gradient (Figure 2.2). The individualistic hypothesis, seeded by Gleason (1939) and developed by Whittaker (1975) and Curtis (1959), argues that the centres and limits of species distributions are scattered non-uniformly along environmental gradients. Thus, no distinct groups of species are predicted to exist, which precludes the recurrence of groups of species in space and time. A more accurate depiction of Clements' hypothesis is given by clusters of species abundance curves with some species spanning more than one cluster and where overlap between communities occurs at the boundary between two communities (Collins, et al., 1993; Whittaker 1975).

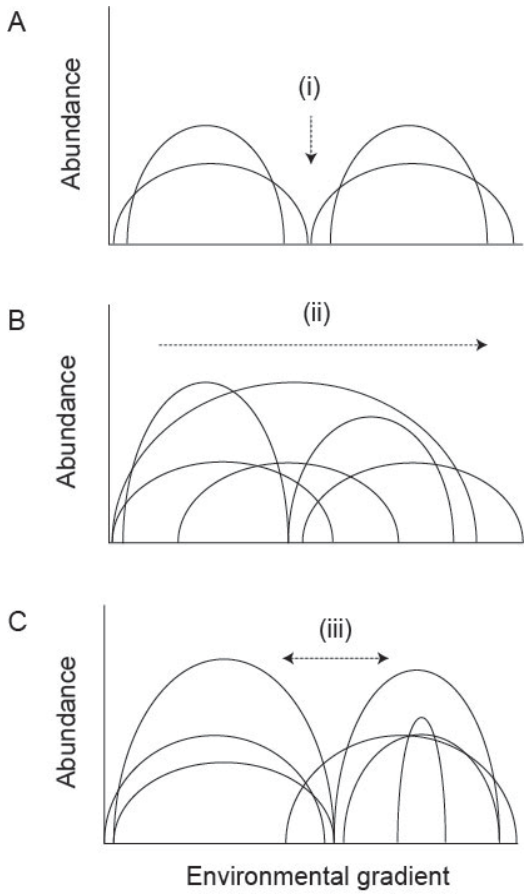

Figure 2.2. Schematic representations of (A) Clements' community-unit hypothesis where two discrete communities can clearly be identified and are separated by a 'hard' boundary around point (i); (B) Gleason's individualistic perspective where no discrete communities can be identified due to continuous environmental variability (ii); (C) An amalgamation of the two concepts that permits both strongly identifiable communities and individualistic distributions that overlap at the boundary.

Two polarised types of biome boundaries can be identified, one being 'hard' the other 'soft' (Figure 2.3.) (Cumming, 2011; Holland, et al. 1991; Hobbs, 1986; Whittaker, 1960; van Leeuwen, 1966). Hard boundaries are zones of relatively rapid change between two plant communities termed 'ecotones' here. They are typically characterised by strong biotic interactions, but can also result from abiotic controls such as stark substrate contrasts. Soft boundaries, in contrast, can be referred to as ecoclines. This type of boundary is often characterised by more gradual transitions between plant communities and typically correspond to some progressive change in an environmental or biotic gradient (Kent, et al.1997). van der Maarel (1990) proposed a third category of boundary comprised of overturning amongst a 'mosaic'

of sub-communities. Interestingly, Kent at al.(1997) suggest that soft ecotones are likely to be more stable than hard ones because their species distributions tend to be determined by natural gradients such as climate, rather than disturbances linked to anthropogenic land use.

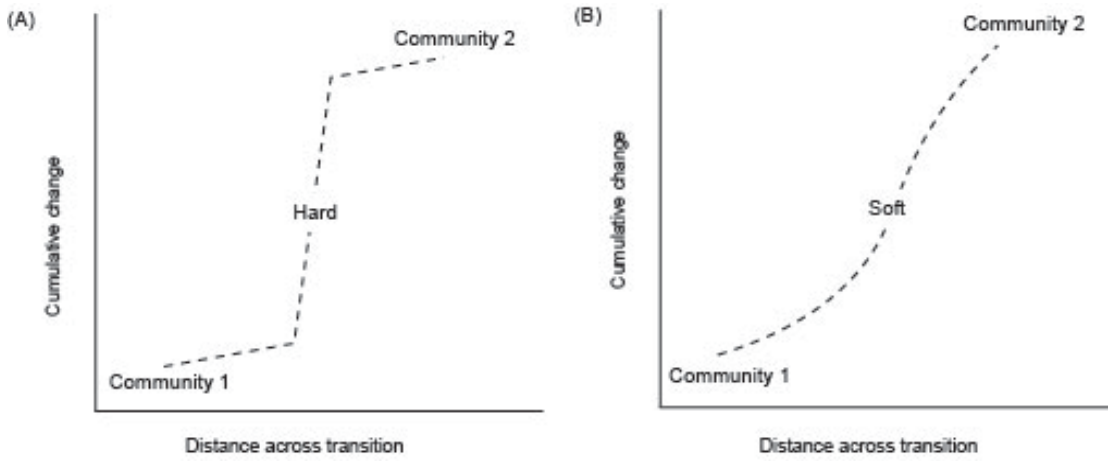

Figure 2.3. Schematic representation of cumulative change in vegetation (structure, function, species composition, etc.) across (A) an 'ecotone' (sharp boundary); (B) an ecocline (gradual boundary). Adapted from Kent et al. (1997).

Biomes are said to be major selective biological filters (Crisp, et al. 2009). Their constituents tend to have shared evolutionary histories, which leads to the possession of similar life-history traits and results in alteration of the abiotic and biotic environment and niche construction (Linder, et al. 2012). This in turn modifies environmental filtering processes and restricts species immigration (Slingsby, et al. 2014). Upon arrival in a recipient community, an immigrant species is confronted with the challenges of a new environment (Potts, et al. 2015). In addition to the genetic, life history and reproductive attributes that facilitate establishment of an initial population, the immigrant must rapidly adapt to the potentially novel biotic and abiotic parameters and variables. Some level of pre-adaptation is obviously advantageous, therefore lineages derived from areas where abiotic and biotic conditions similar to the destination environment prevail are clearly at an advantage (Verboom, et al. 2014). It might be expected therefore that species with similar life-history/ functional traits will tend to group together forming discrete entities (i.e. Clementsian) with hard, impenetrable boundaries resulting from ecological filtering processes.

2.2. ECOLOGICAL RESILIENCE AND ALTERNATIVE STABLE STATES

The capacity of an ecosystem to absorb environmental perturbations through internal feedbacks to maintain a quasi-stable state is known as resilience. The concept of resilience has recently been dissected to emphasise the distinct ways in which ecosystems absorb or respond to environmental perturbations. Two distinct, measurable components of resilience in an ecological entity (i.e., a population, community, ecosystem, formation or biome) are recognised. First, 'resistance' refers to the capacity of a system to withstand a disturbance and maintain its original qualities. Second, 'recovery' is the capacity to return to or restore its original character following a change in response to disturbance (Oliver, et al. 2015) (Figure 2.4). As such, system 'resilience' can be viewed as a general concept, whereas the two components resistance and recovery represent measurable responses to environmental perturbations (Hodgson, et al. 2015).

If the resilience of an ecosystem is exceeded the system may reorganise into one of multiple possible alternative quasi-stable states, each with its own set of reinforcing negative feedbacks (Holling, 1973). Ecological thresholds define the point at which a community switches from one quasi stable state to another (Scheffer, et al. 2001). Alternative stable states can be characterised by the presence of differing plant functional types, vegetation structure, biomass and percentage cover, as well as by contrasting ecological processes (e.g. fire prone verses inflammable stands) (Anderies, et al. 2002; Beisner, et al. 2003; Gillson and Duffin, 2007). More recently, transitions between states have become known as regime shifts, where relatively long periods of stability are interrupted by large, rapid reorganisation of a system occurs resulting in a qualitatively different state (Brook, et al. 2013; Carpenter, et al. 2011; Foley, et al. 2003; Scheffer and Carpenter, 2003; Scheffer, et al 2009).

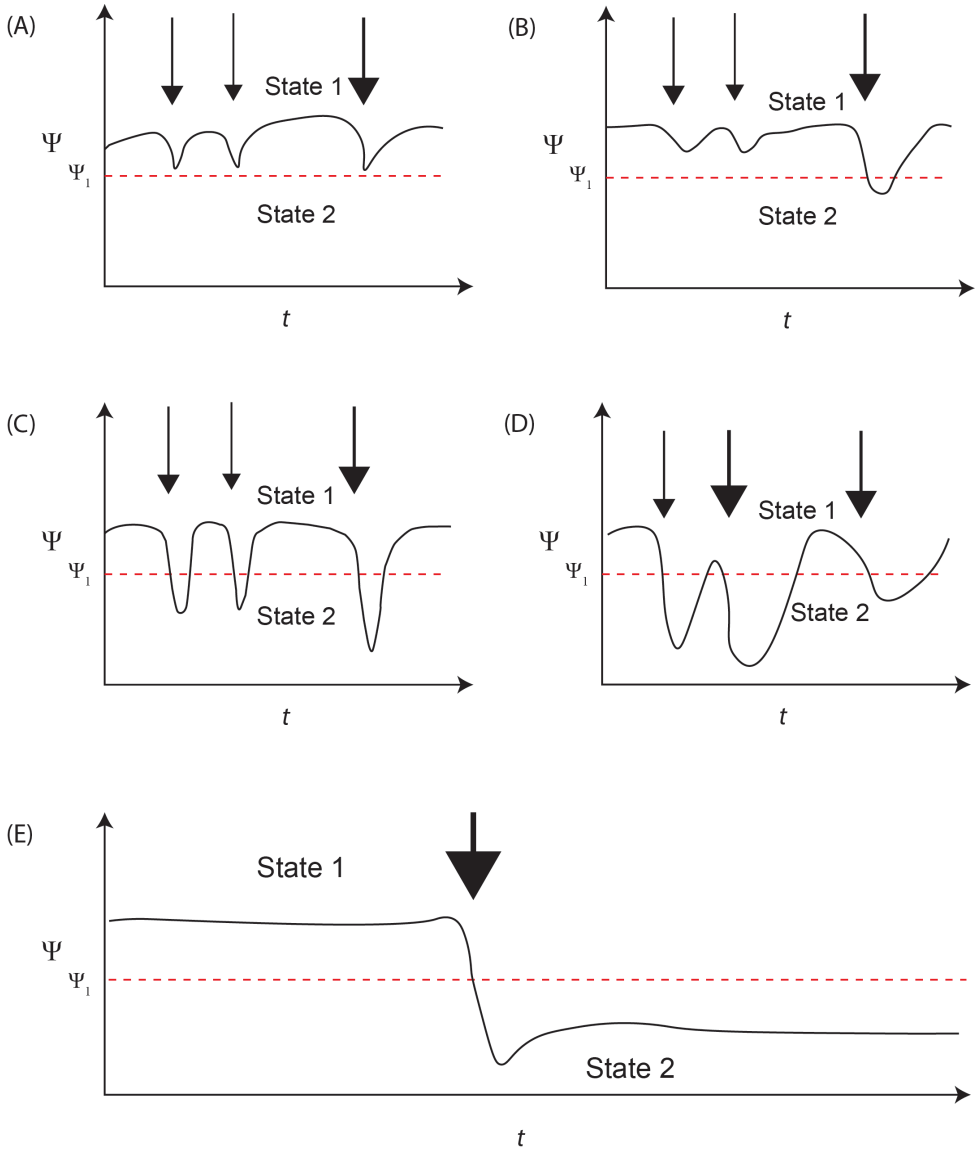

Figure 2.4. Resilience, resistance and recovery. Schematic diagrams representing varying resilience characteristics for a hypothetical ecosystem parameter or function (Ψ) to environmental perturbations (arrows). Panel (A) represents a system with high resistance and rapid recovery; panel (B) represents a system with high resistance but slow recovery; panel (C) represents a system with low resistance but rapid recovery; panel (D) represents a system with low resistance and slow recovery; panel (E) represents a system in which resilience is lost resulting in reorganisation around an alternative state. The dashed red line represents a threshold (Ψ^{l}) between alternative system states (Adapted from Oliver, et al. 2015).

Historically, alternative stable states have been viewed from two perspectives. The 'community perspective' (Drake 1991; Lewontin 1969) emphasises internal changes in ecosystem populations and views the environment as fixed in some way. Perturbations are applied to state variables by biotic processes and, if large enough, may lead to a state shift. This scenario has often been described using the ball-in-cup

analogy (Figure 2.5), whereby the ball is pushed over a hill in a constant landscape to the domain of attraction of an alternative state. The 'ecosystem perspective' (May 1977, Scheffer et al 2001) focuses on the effects of environmental change on the state of communities. Changes in model parameters (e.g. climate) drive changes in state variables (e.g. fire), which may induce or alter propensity to a state shift (Figure 2.6). It is increasingly recognised that processes accommodated within both these frameworks may interact to determine system dynamics, whereby changes in ecosystem parameters influence the susceptibility of a system to a state shift caused by community-level perturbations (Beisner et al 2003; Vetter 2009).

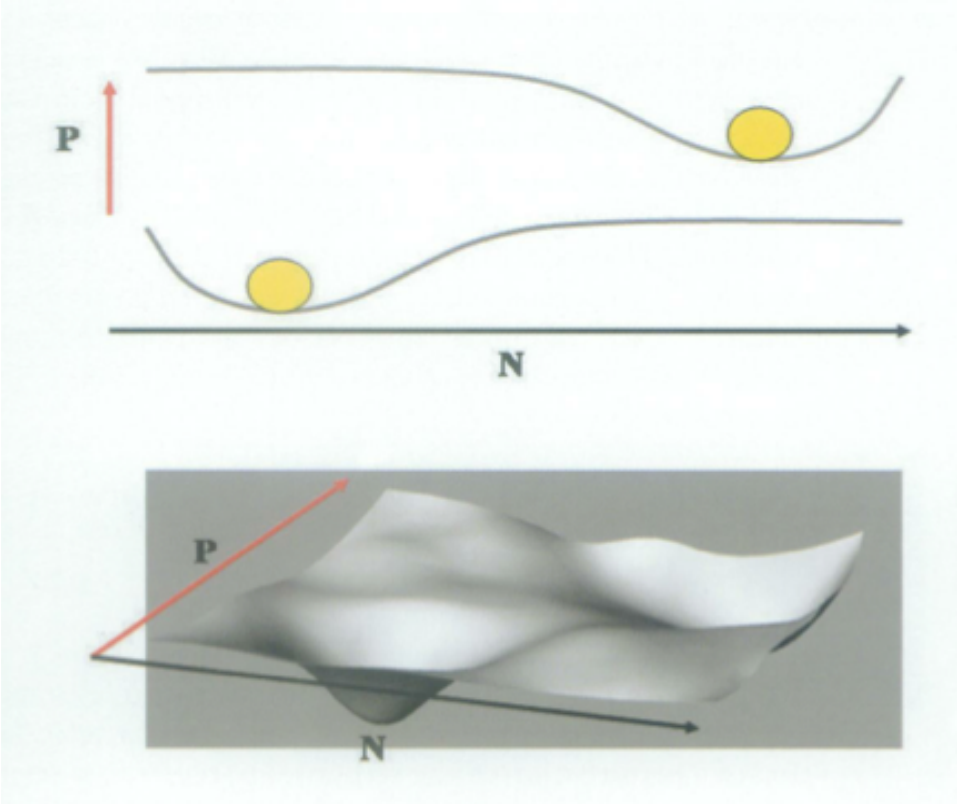

Figure 2.5. Alternative stable states and the 'ball in cup method'. The distinction between the community and ecosystem approaches to alternative stable states theory concerns the treatment of state parameters and state variables. In the ecosystem perspective (top) a parameter (P) is changed according to the vertical red arrow in response to an external factor. The community equilibrium point moves along the horizontal axis (N) driven by the parameter change. There are no interactions between the state variable and parameter. In the community perspective (bottom) the former parameter P is now a state variable included in the model, because P is subject to rapid feedback from the state variables. Perturbations caused by forces external to the variables N and P can move the community ball around on the landscape. The landscape is now defined jointly by N and P and remains fixed (Figure and caption from Beisner, et al 2003).

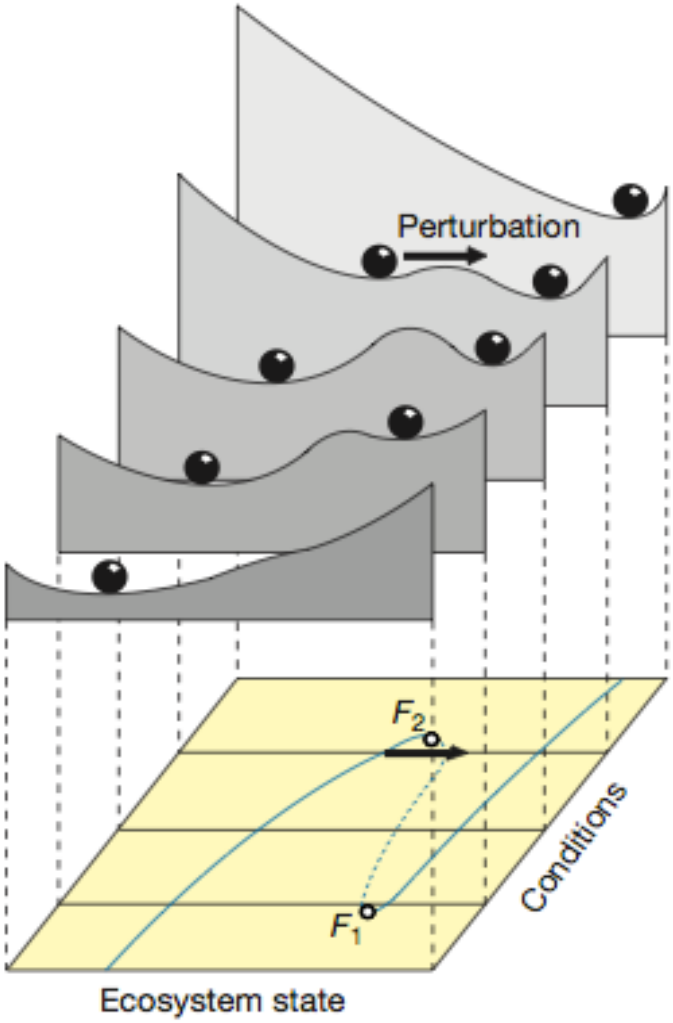

Figure 2.6.Classic bifurcation model of Scheffer and Carpenter (2001). The five 'stability landscapes' depicted represent the multiple alternative stable states and their basins of attraction at five different external conditions. Stable states correspond to valleys; the unstable middle section of the folded equilibrium curve corresponds to a hill. If the size of the attraction basin is small, resilience is small and a perturbation may cause a comparatively large shift to alternative stable state (Figure and caption from Scheffer, et al. 2001).

Ecologists have generally rejected the ideas of Clements, and tend to be sceptical of the idea of communities as homeostatic entities (Connell and Ghedini 2015). This seems paradoxical, given that the widely applied concepts of alternative stable states and regime shifts in ecology are underpinned by recognition for strong internal ecological organisation and feedback processes (Anderies, et al. 2002; Beisner, et al. 2003; Brook, et al. 2013; Carpenter, et al. 2011; Drake 1991; Foley, et al. 2003; Gillson and Ekblom, 2009; Holling 1973; Lewontin 1969; May 1977; Scheffer and Carpenter, 2003; Scheffer, et al 2009, 2001; Vetter 2009). Indeed, application of the

alternate stable states model to vegetation change at biome boundaries incorporates an assumption that biomes are, and will remain, cohesive organisations of species through space and time due to negative feedback control. This assumption is also evident in predictive biome distribution models (Bomhard et al 2005; Hannah et al 2005; Midgley and Thullier 2007; Midgley et al 2005, 2003). Such simplistic approaches have been criticised for not incorporating different reproductive strategies, differential dispersal rates and capabilities, and the breakdown of reproductive and other biotic relationships (Desmet, 2007; Gavin, et al 2014).

2.3. ECOLOGICAL DYNAMICS AND THE PALAEOECOLOGICAL RECORD

Observations of species responses to environmental change in the fossil record have been interpreted as demonstrating that vegetation response to climatic change is individualistic, supporting the Gleasonian as opposed to the Clementsian view of community assemblage (Birks and Birks, 1980; Delcourt and Delcourt, 1988; Prentice 1992; Whittaker, 1975). For example it has been shown that, in Europe and North America, Late-Quaternary climate warming caused the distribution of individual species to change in differing rates and geographical direction (Delcourt and Delcourt, 1988; Graham and Grimm, 1990; Prentice, 1992). These differing responses resulted in dynamic community assemblage patterns and ecosystems without modern analogues (so called ‘no-analogue ecosystems’) through the Late Quaternary period in North America (Jackson, 2006) and in Europe (Bennett and Birks, 1990). Co-occurrence of species is dependent on overlap in multi-dimensional ecological and biogeographic space, making repeated overlaps less likely (Jackson and Williams, 2004).

It may seem surprising, then, that some palaeoecologists have interpreted fossil ecosystems as exhibiting evidence for the existence of alternative stable states. It is important to emphasise that the overwhelming majority of palaeoecological research used to support the Gleasonian perspective comes from Europe and North America, which were both covered by ice masses during glacial phases and re-colonised during interglacials (Lowe and Walker, 1997). Many species were forced adapt by migration

on large, continental scales to refugia, which in effect emphasised individual trait differences such as differential dispersal rates (Prentice, 1992). Much of the rest of the world, particularly tropical and subtropical regions and most of the global south, experienced comparatively less extreme environmental change (Chase and Meadows, 2007). The majority of Earth's biodiversity may therefore possess contrasting traits and resulting dynamics. Southern hemisphere perspectives on the Clementsian/ Gleasonian debate and ecosystem organisation are therefore needed.

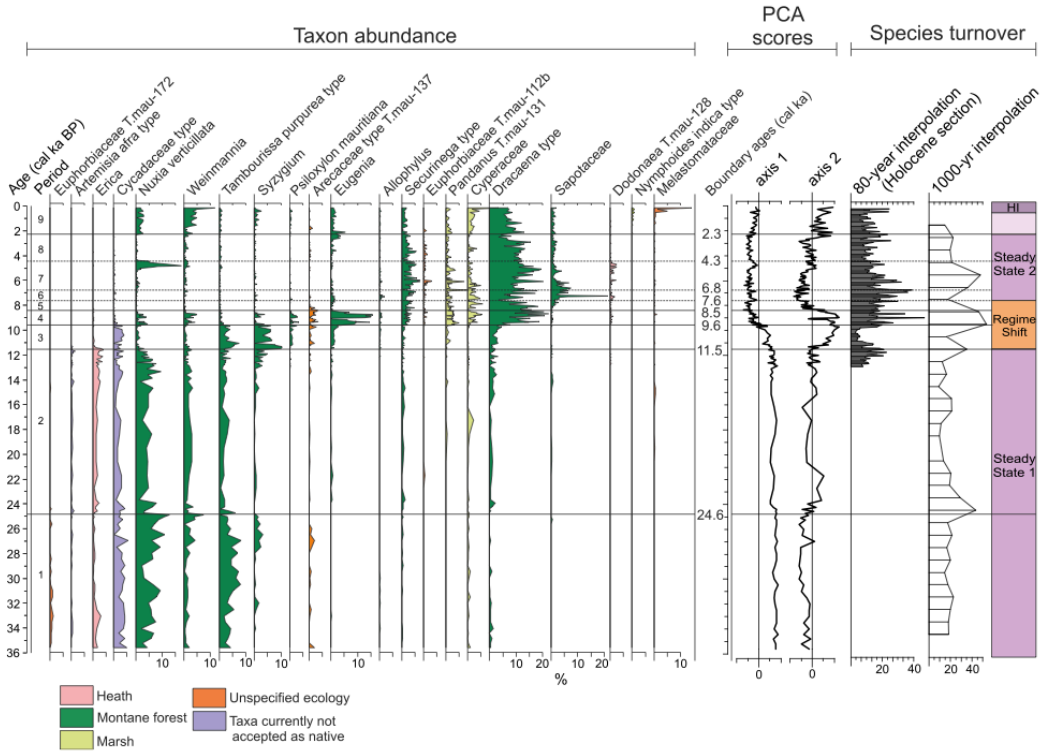

Figure 2.7. Percentage pollen diagram of Kanaka-1 (DeBoer, et al. 2013). Also plotted: depth, Principal Components Analysis (PCA) scores and calculated species turnover scores between sample intervals.

DeBoer, et al. (2013) interpret a Late Quaternary pollen record from Mauritius as reflecting two alternative quasi-stable states interrupted by a relatively rapid regime shift between open, wet forest Last Glacial state to a stable closed, stratified, tall forest Holocene state in response to transgression of an ecohydrological threshold (Figure 2.7). Each state persisted for several millennia while the regime shift - or transition between the two alternative states - occurred over relatively shorter centennial timescales. Gil-Romera, et al. (2010) highlight two records from southern

Spain (Carrión, et al. 2003; Martin-Puertas, et al. 2008) that express varying types of resilience (Figure 2.8). At Zoñar, the system closely tracked changes in aridity between 3,300 and 700 cal yrs BP. This is manifested in oscillations between dominance of xerophytic and mesophytic vegetation where phases of stability are interrupted by relatively rapid transitions. Stabilising internal feedback processes (i.e. resilience) can be viewed as weak, however, as the system's state varies in response to extrinsic climate forcing. In contrast, the pollen record at Gádor shows several quasi-stable phases superimposed upon a more obvious directional trend in response to aridity from around 6,000 cal yrs BP. In the latter case, each successive phase appears to show strong cohesion, but unidirectional change in ecosystem parameters (moisture) induces resilience loss resulting in successive state shifts.

The studies of both DeBoer, et al. and Gil-Romera, et al. emphasise the importance of temporal scale in describing the resilience of ecosystems. On relatively short neontological timescales (i.e. years to decades) systems may appear to be cohesive units that interact through negative feedbacks to maintain resilience. By studying plant communities and ecosystems on palaeoecological scales (i.e. decades to millennia) their deeper dynamics can be revealed (Jackson 2006; Williams and Jackson, 2004). Conversely, looking at too short a timescale might result in misleading impression of instability as erratic variability in ecological parameters (e.g. inter-annual temperature extremes) do not necessarily lead to lasting ecosystem change.

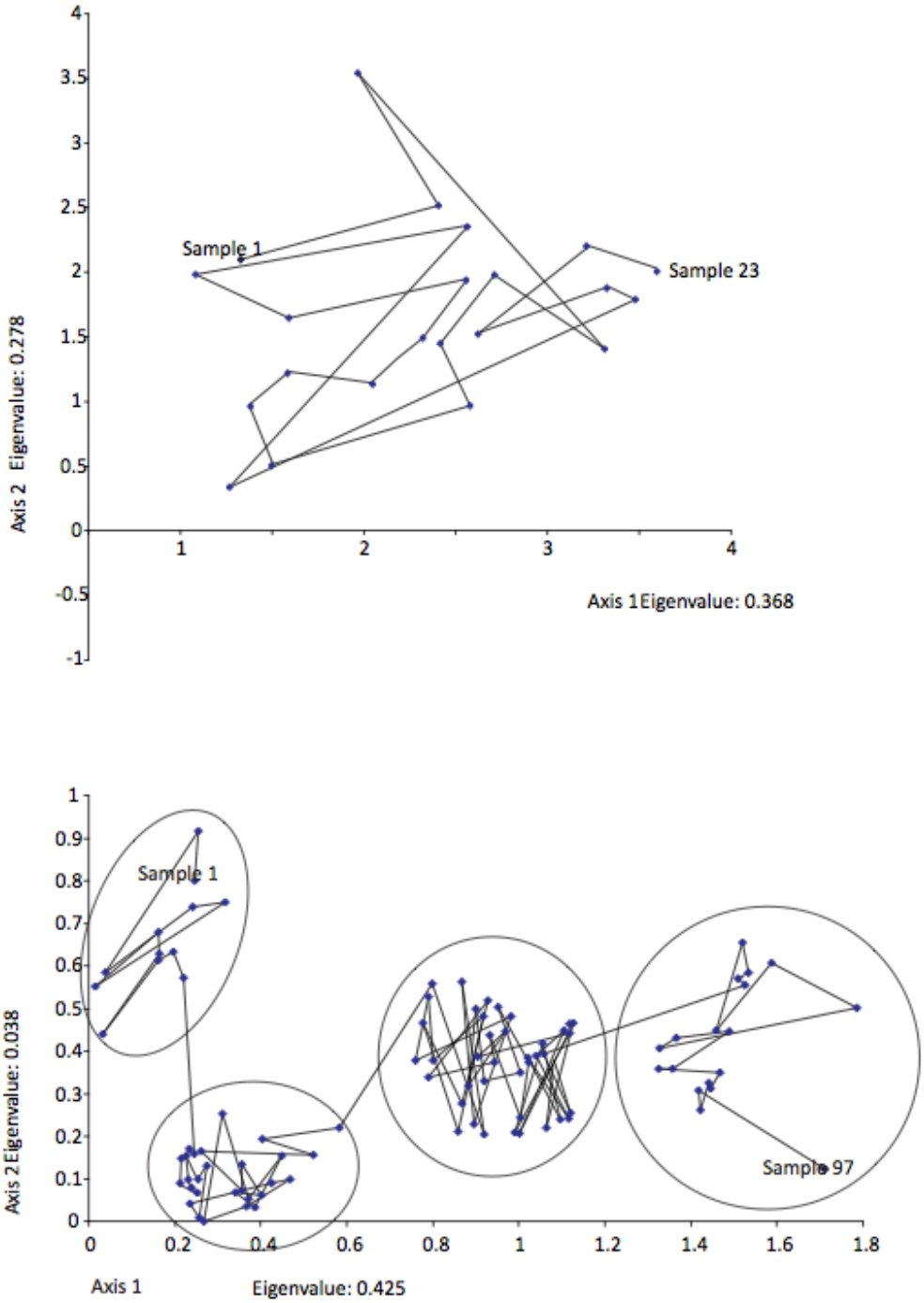

Figure 2.8. Detrended Correspondence Analysis ordinations for Zoñar (top) and Gádor (bottom). The samples are joined with a line and the oldest and youngest samples are labelled (need to give ref and accreditation here).

2.4. THE ECOLOGY OF THE FYNBOS-SUCCULENT KAROO BIOME BOUNDARY

Fynbos is a sclerophyllous shrubland composed of reed-like graminioids, short shrubs and taller shrubs in varying combinations (DeBano 1998). The main definitive plant groups are Restionaceae, Proteaceae, Ericaceae, and geophytes, the latter principally belonging to the Iridaceae. The particular combination of these groups is used to class fynbos into one of five groups: restioid, proteoid, ericaceous, asteraceous or grassy fynbos (Figure 3.9.) (Cowling 1995). Succulent karoo is dominated by dwarf leaf-succulents of the Aizoaceae, Euphorbiaceae and Crassulaceae. Also of prominence are members of the Asteraceae, Iridaceae and Hyacinthaceae. Annuals belonging to the former group contribute significantly to the spectacular springtime floral displays for which the biome is renowned (Figure 3.10) (Mucina et al 2006). The transition between these two vegetation types is almost always interrupted by a narrow zone of vegetation known as mountain renosterveld. This vegetation type is also classified as belonging to the fynbos biome (Rebelo et al 2006; Low and Rebelo 1998; Rutherford and Westfall 1986; also see Chapter 3.1). Questions of its origins, associations and status as a biome in its own right are topics of current interest (Bergh, et al. 2014, 2007; Curtis, 2013). It is often distinguished floristically by the dominance of *Elytropappus rhinocerotis*, a 1-2 m tall asteraceous shrub. Renosterveld graminoid composition also contrasts with that of fynbos where Poaceae typically forms a dense understory and Restionaceae is almost always absent (Rebelo et al 2006).

The fynbos-succulent karoo transition almost always occurs where mean annual precipitation (MAP) is around 200-300 mm, where fynbos is the relatively mesic vegetation (fynbos MAP = 287 mm to 1384 mm, succulent karoo MAP = 150 to 209 mm) (Figure 2.10) (Agenbag et al 2008, Agenbag, 2006; Rebelo et al 2006). Results from a number of studies (Carrick 2001, 2003; Jacobsen et al 2009; Lechmere-Oertel and Cowling 2001) support the assertion that fynbos expansion into karroid habitat is inhibited by relatively low tolerance of aridity stress. For example, fynbos species have been indicated as less resistant to drought induced xylem cavitation (Jacobsen et al 2009), and succulent karoo species showed less response to moisture regime variation in reciprocal transplant experiments (Lechmere-Oertel and Cowling 2001).

Succulent taxa such as the Aizoaceae incorporate thick water storing tissues within their main photosynthetic organs, which buffer against desiccation during drought (Vendramini et al 2002). Temperature change is also likely to be an important variable in vegetation distribution at the biome boundary, both independently through changing thermal stress and the proximity of thermal thresholds, and in combination with precipitation by altering the timing and extent of soil moisture availability and the vapour pressure deficit (Midgley and Thuiller 2007).

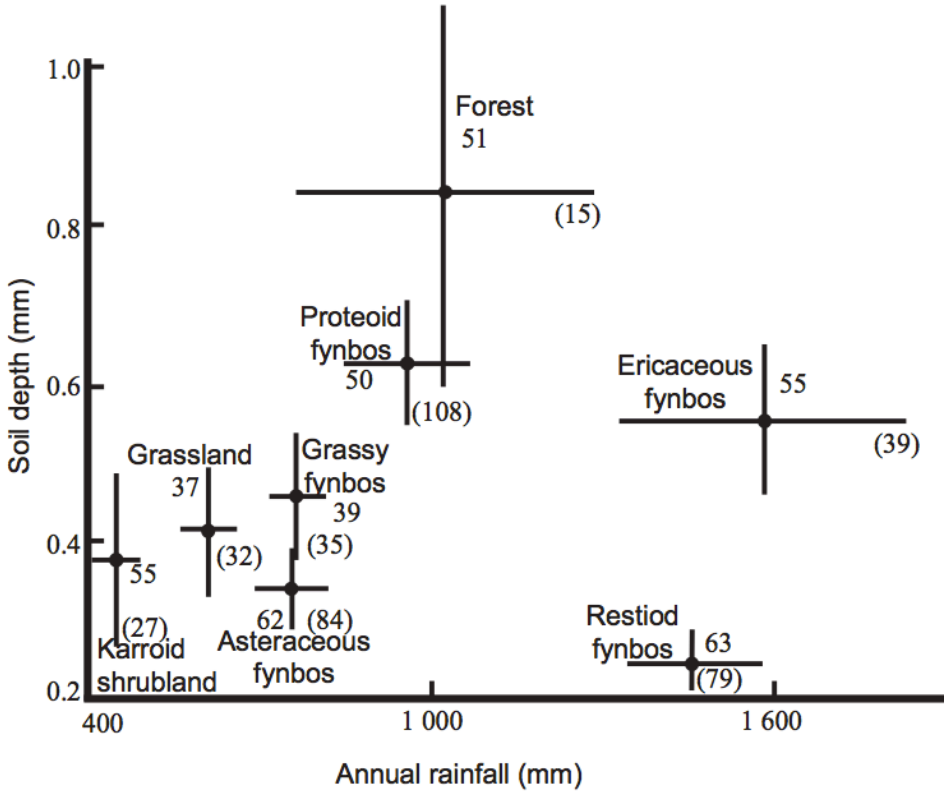

Figure 2.9. Direct ordination by climate and soil depth of fynbos sub-types and adjacent biomes in the south western Cape (figure from Rebelo, et al. 2006).

Figure 2.10 Various fynbos sub-types. A: proteoid fynbos dominated by Leucadendron xanthoconus *(Proteaceae) and* Phaenocoma prolifera *(Asteraceae) at Potberg; B: Proteoid fynbos with tall, scattered Protea nitida (Du Toitskloof). C: Coastal asteraceous fynbos* Phaenocoma prolifera *(Betty's Bay) D: grassy fynbos with* Oldenburgia grandia *(Asteraceae) in the foreground (Grahamstown); ericaceous fynbos dominated by* Erica laeta *(Cape of good hope); F: restiod fynbos with* Thamnocortus spicigerus *(Agulhus Plain). (Images from Rebelo, et al. 2006).*

Figure 2.11. Namaqualand spring bloom. Commercial farmland in the Kamiesberg dominated by annuals of Asteraceae and Poaceae (A.J. MacPherson).

Figure 2.12. Namaqualand Mountain Renosterveld. Commercial livestock farmland in the uplands of the Kamiesberg dominated by Elytropappus rhinocerotis *('renosterbos'). (A.J. MacPherson)*

Competition has also been suggested as an important determinant in biome distribution. In the reciprocal transplant experiment by Lechmere-Oertel and Cowling (2001), karroid species showed less sensitivity to soil texture and nutrient availability, leading to the suggestion that they are outcompeted at the biome boundary where moisture availability is not limiting to fynbos growth (Lechmere-Oertel and Cowling 2001). Therefore, where moisture is ample competitive exclusion may become more deterministic at the fynbos-succulent karoo boundary. Carrick (2003) identified rooting system partitioning between karroid woody shrubs (deep rooted) and succulent shrubs (shallow rooted) in the Kamiesberg region, suggesting coexistence by differentiation (Walter 1971). The prevalence of such coexistence strategies may be indicative that biotic interactions are less important in these semi-arid systems than are abiotic stressors such as drought. Interpretations of niche separation based on models of root system partitioning in arid lands have received criticism in that they neglect root system plasticity, potential lagged response to rainfall events, the vagaries of plant phenology, and explicit precipitation thresholds that occur within highly variable soil moisture environments (Ogle and Reynolds 2004; Schwinning et al 2004). However, the effects of competition cannot be discounted altogether. Under scenarios of increasing aridity stress, the competitive advantage of fynbos species over those of the succulent karoo would be expected to diminish. Importantly, this highlights that of biotic relative to abiotic parameters become less important in determining plant distributions as aridity increases.

Fynbos is fire prone and adapted, but burning is highly destructive in succulent karoo (Bond 1997; Cowling et al 1995; Esler, et al 2015). At the boundary, fire prevalence may dominate biome boundary dynamics; only in its absence will climate, soil or competition factors become deterministic. Indeed, it has been observed that succulent karoo replaces fynbos when vegetation cover and the accumulation of combustible biomass become too low to carry fire (Rebelo et al 2006). Growth of succulents in fire-free microhabitats, such as rocky outcrops (Figure 2.13), within fynbos further suggests that fire plays a dominant role in biome boundary dynamics (Anderson 2008). The persistence of succulents in fire-free microhabitats has also been

documented in other semi-arid systems (Thomas and Goodson 1992). Colonization of fynbos vegetation by succulents in the absence of fire would greatly decrease vegetation flammability, thereby suppressing fire and fynbos regeneration, a positive feedback loop that would increase resilience of succulent karoo (Rebelo, et al. 2006). An alternative view might be that, as fynbos is drought limited, fire responds to rather than determines vegetation type at the biome boundary.

Renosterveld burns more frequently than fynbos (typical fire free intervals are 3-10 years and 15-20 years, respectively) (Rebelo et al 2006), and tends to stimulate ignition in adjacent fynbos vegetation. Kamiesberg Mountain Fynbos may require such an ignition source due to the small size of the vegetation patches and the associated low likelihood of ignition by lightning or rock falls. Renosterveld can also support a higher biomass of herbivores (particularly grazers) than fynbos because of its grassy understory. This is supported by data from rangelands in the Kamiesberg that demonstrate the potential of herbivores to significantly alter plant biomass (Anderson and Hoffman 2007). It has been hypothesised that intense grazing suppresses fire in renosterveld, allowing invasion of the transitional zone by succulents, thereby acting as a fire suppressant and potentially also removing an important ignition source for fynbos. Less frequent burning may then allow succulents to establish between senescing fynbos plants, further suppressing fire and creating a feedback loop in favour of succulence, and potentially driving a state transition between fynbos and succulent karoo (A.G. Rebelo, pers. comm.; Cowling and Holmes 1992).

A strong correlation can be observed between fynbos-succulent karoo distribution and substrate type (Quick et al 2011). Over much of their distribution, succulent karoo is distributed on soils derived from lowland shale deposits of the Malmesbury formation that are high in clay and silt content, and are relatively nutrient rich (Rebelo et al 2006). These fine textured soils have a high internal surface area, and as such greater potential to retain water, which reduces moisture availability to plants (Marshal and Holmes 1979). Fynbos is commonly distributed on nutrient leached sandy soils derived from the quartzitic sandstone mountain ridges of the Cape Fold Belt (Rebelo et al 2006). In such coarse textured soils, water is more freely extractable as it is

stored in capillaries between the grains (Brady 1974). Renosterveld commonly persists on an intermediary of shale and sandstone alluvium that is less subject to nutrient leaching than higher altitude Fynbos (Rebelo 2006). It has been hypothesised that a rainfall-induced nutrient-leaching gradient is the prime determinant in separating fynbos and renosterveld (Cowling et al 1997). There lacks consensus whether soils are most important in water retention or nutrient characteristics (Esler, et al 2015; Agenbag 2008; Lechmere-Oertel and Cowling 2001).

Figure 2.13. Succulents occupy fire-free rocky habitat in the Kamiesberg. Lampranthus *sp. is common in fire free habitat in the Kamiesberg uplands (Image: A.J. MacPherson).*

Boundaries between fynbos and succulent karoo are typically characterised by sharp transitions with associated oligotrophic and mesotrophic soils, respectively, as well as the aforementioned gradual climate transition. Esler et al. (2015) sought to disentangle the relative roles of climate and soil type in determining the biome boundary in a reciprocal transplant approach at Jonaskop in the Western Cape.

Their results, similar to those of (Lechmere-Oertel and Cowling 2001), suggest that succulent karoo species are neither edaphically nor climatically constrained from

habitat typical of fynbos vegetation along this elevation gradient. In contrast, fynbos species are strongly limited both edaphically and climatically from growing under conditions associated with succulent karoo. The authors therefore suggest that succulent karoo elements may be excluded from fynbos by competition or fire, and that the latter is most likely responsible for maintaining the sharp boundary. Fire would strongly exclude fire sensitive succulent karoo species from fynbos, while both mesotrophic soils and climate together would strongly exclude fynbos species from succulent karoo. The relative climate, soil and disturbance affinities might therefore provide an explanation for the relative distributions of the fynbos and succulent karoo biomes, as well as the hard ecotone type nature of the boundary. This is suggestive of Clementsian system organisation.

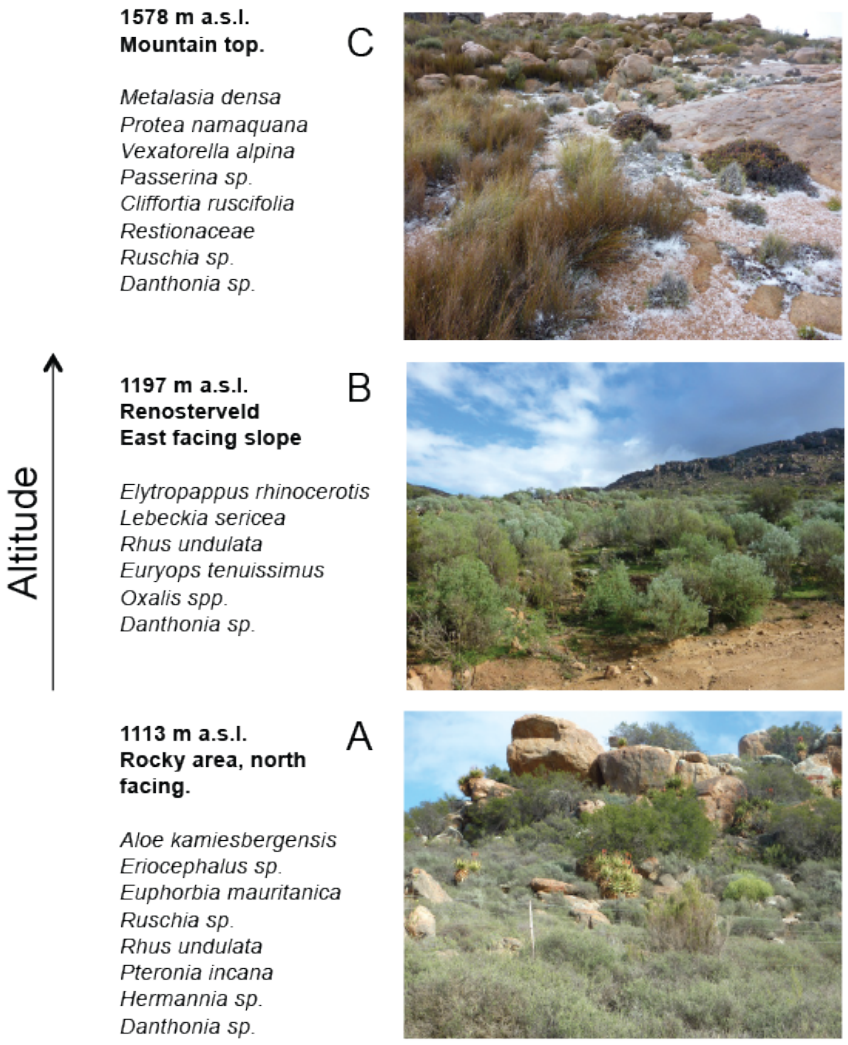

Figure 2.14. Vegetation distribution across an altitudinal gradient in the Kamiesberg. A: Succulent karoo (Kamiesberg Mountain Shrubland); B: renosterveld (Namaqualand Granite Renosterveld); C: fynbos (Kamiesberg Mountain Fynbos) (Rebelo, et al. 2006). (Images A.J. MacPherson).

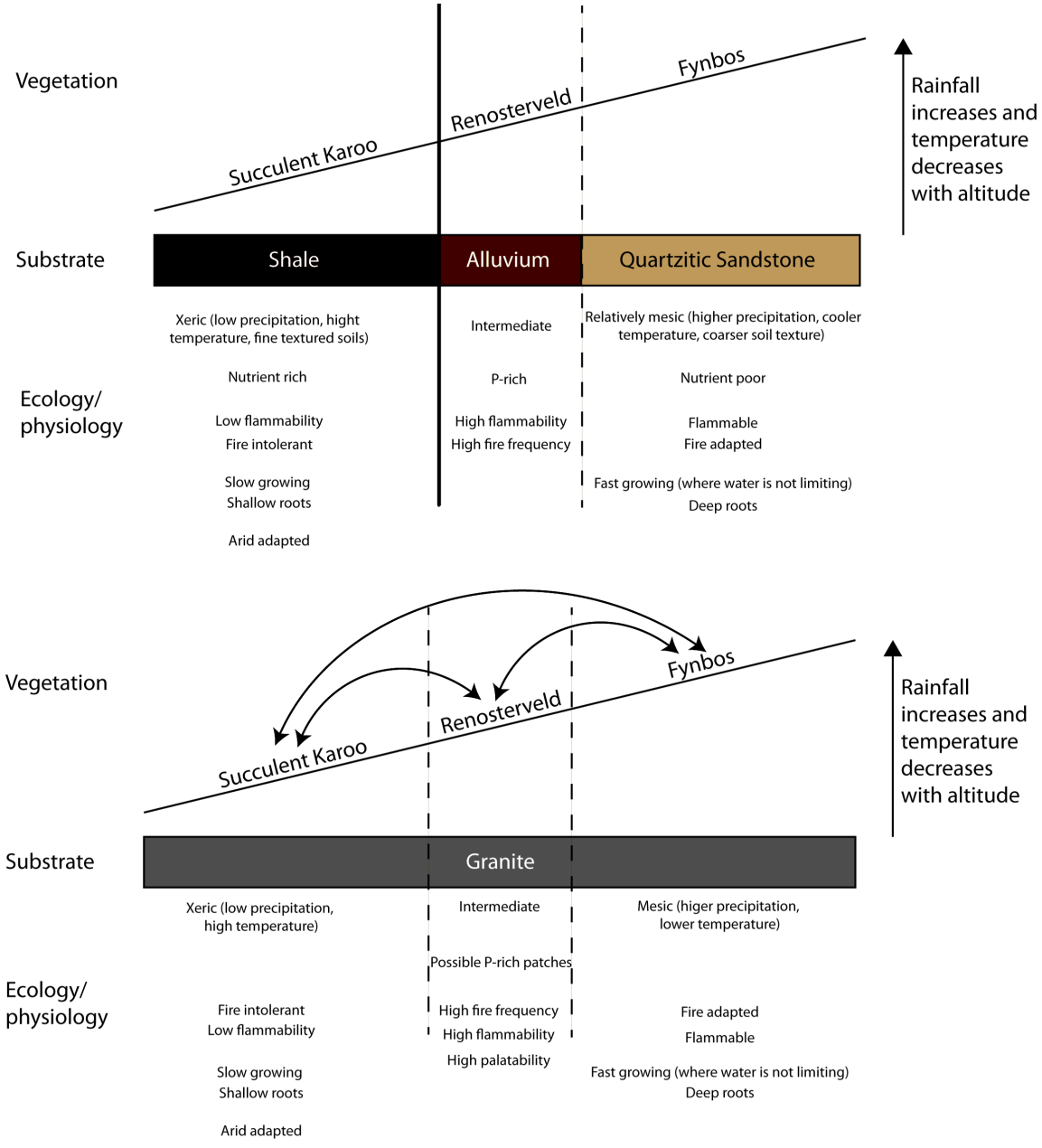

Figure 2.15. Schematic representation of the fynbos-succulent karoo boundary. Typically the boundary is sharp (top) but in the Kamiesberg it is diffuse (bottom) suggesting soft ecological controls.

The relationships between vegetation and substrate type in the Kamiesberg Mountains of Namaqualand, towards the northern extremity of fynbos distribution, are somewhat of an exception to the patterns described above. Here, similarly to across most of the

GCFR, the fynbos-succulent karoo transition occurs along an increasing altitudinal gradient (Figure 2.14) where MAP = 200 to 300 mm. It is exceptional that this transition occurs across granite-derived soils rather than those that developed from quartzitic sandstone or bokkeveld shales (Figure 2.15). While over much of the distribution the fynbos-succulent karoo boundary is characterised by a sharp boundary, likely resulting from the effects of substrate contrasts and fire (Esler, et al 2015), the interface between the two biomes in the Kamiesberg is more diffuse (Rebelo, et al. 2006). At present, there is little published data relating to soils of the Kamiesberg Mountains. Anderson (2008) surveyed soil chemistry and texture among a number of vegetation types along an altitudinal gradient in the Kamiesberg (excluding fynbos proper, which occurs only on the highest mountain tops, but including renosterveld). Upland habitats, particularly renosterveld, were characterised by high soil percentage organic carbon and nitrogen content, which is probably a function of higher vegetation cover (Anderson 2008). The diffuse nature of the boundary conforms to the ecocline type defined by Kent, et al. (1997), and is suggestive of loose system organisation where species are distributed along a climatic gradient. However, the persistence of succulents in fire-free habitat is suggestive of a hard biome boundary. Both Clementsian and Gleasonian system organisation is therefore evident in the Kamiesberg depending upon the scale of measurement.

Observations of rapid, non-linear and non-reversible changes in semi-arid rangelands as a result of grazing, drought and fire have stimulated debate as to whether such ecosystems exhibit alternate stable state characteristics (Rutherford and Powrie 2010; Vetter 2009, 2005). Rutherford and Powrie (2010) highlight how intense grazing in Namaqualand has led to the formation of resilient species pools, suggesting the existence of alternate stable states. In the Kamiesberg, alternate stable states may be characterised by shifts between fynbos and succulent karoo, as well as changes within biomes, such as a shift to dominance of *Galenia africana* in succulent karoo in response to heavy grazing or to *Elytropappus rhinocerotis* in renosterveld and fynbos (Figure 2.12) (Curtis, 2013; Keeley, et al 2012; Todd and Hoffman 2009). It is suggested here that vegetation in the Kamiesberg may be more susceptible to shifts in ecosystem state than elsewhere in the biome because (i) biome boundary transitions occur across one substrate type, reducing the resilience afforded by substrate-derived

ecosystem affinities and; (ii) because the dominant ecological/ physiological processes are more dynamic.

2.5. THE ECOLOGY OF THE FYNBOS-AFROTEMPERATE FOREST BIOME BOUNDARY

Indigenous forests of South Africa are rare, covering <1 % of the country's land surface. Most are island archipelagos set amongst larger-scale matrixes of the fynbos, albany thicket, grassland, savanna biomes and transformed biomes such as agricultural land (Mucina and Geldenhuys, 2006). Only one of the twelve forest types identified in the national vegetation classification (Mucina and Geldenhuys, 2006; also see Rutherford and Westfall, 1986) qualifies as a biome in its own right: the Southern Cape Afrotemperate Forest (Figure 2.16). These are tall, multilayered forests dominated by yellowwoods (*Podocarpus* spp.) that persist down to sea level at ~34^{o}S, and are comparable to warm-temperate forests in the northern hemisphere such as those in East Asia and the south western United States. The largest single forest patch (25,706 ha) is the Tsitsikama Forest in the southern Cape. This forms part of a still larger complex of 60,560 ha at about 34° S, spanning 22° to 24° 30' E (Geldenhuys 1991) in the southern Cape along the costal plateau between Humansdorp in the east and Mossel Bay in the west.

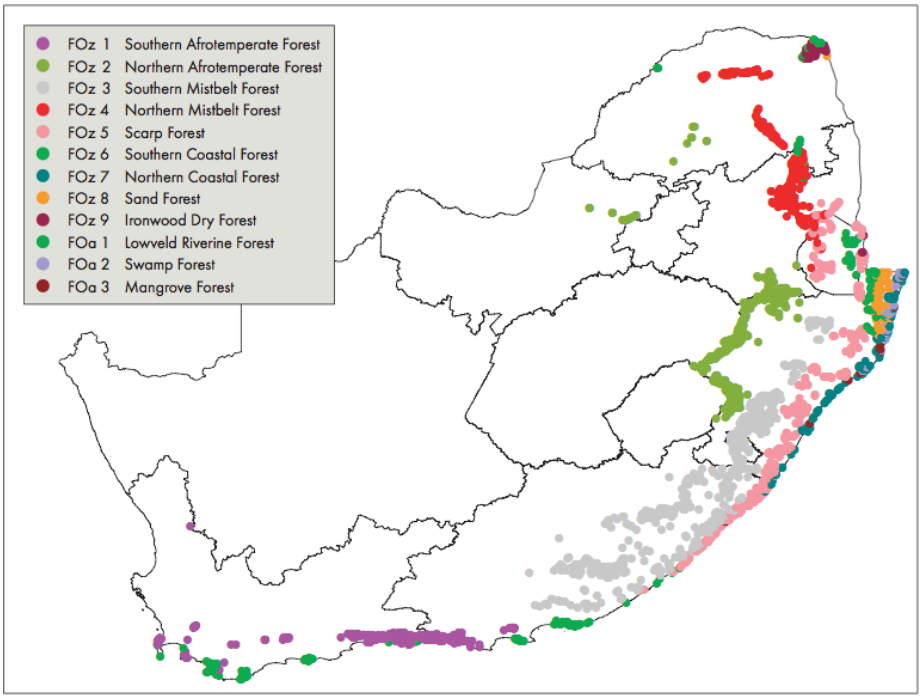

Figure 2.16. Distribution of forest biome sub-types in South Africana and Swaziland.

Forests worldwide, including those of Mediterranean and temperate climate regions, have been indicated as vulnerable to drought. Choat, et al (2012) suggest that trees are, on a global scale, vulnerable to embolism under drought conditions. Specifically, that negative pressure in the xylem results in a phase change from liquid water to water vapour, and the resulting gas globules cause vascular blockages limiting water supply for photosynthesis. They argue that embolism is a key mechanism in vegetation shifts and forest decline as this sets thresholds for stomatal closure, which limits photosynthesis, increases heat and light damage, and exhausts carbon stocks over time. There has historically been a tendency to view forests as most vulnerable to drought and, similarly, that global vegetation distribution is most influenced by climate – and the Cape flora is no exception.

February and Manders (1999) examined the effects of water availability on selected species from fynbos (*Protea repens, P. nitida, P. nerifolia*) and afrotemperate forest (*Cunonia capensis*, *Kiggelaria africana*) in the south western Cape by examining the relationships among plant biomass, vessel size and vessel frequency. The forest species showed lower adaptive capacity than those of fynbos, indicating absence of

traits that might allow persistence in sandstone fynbos habitat that is subject to greater physiological stress than are species in forest habitat. Similarly, Manders (1990, 1992) suggests that seedlings of forest species are likely to be more vulnerable to drought than those of fynbos, possibly because they share a greater vulnerability to xylem cavitation during establishment under summer drought conditions with inadequate shade (E. February, P.T. Manders, A. Scholtz, unpublished data; Coetsee, et al. 2015). Under more favourable conditions some forest species characteristic of the ecotone, such as *Kiggelaria africana* or *Virgilia* spp., could apparently proliferate in the intermediate environmental space with adequate moisture and shade cast by forest trees. Manders (1990) concluded that moisture availability broadly determines fynbos/ forest distribution below a threshold where MAP is <600 mm. Where moisture availability exceeds this, other factors may determine the distribution forest and fynbos.

The southern Cape plateau forests are subject to less extreme summer hydrological stress than elsewhere within the fynbos biome, such as in the south western Cape that experiences extreme summer drought, because precipitation is distributed more evenly throughout the year. In these forests the transition to fynbos occurs without strong association to climatic gradients. Afrotemperate forest persists where mean annual precipitation (MAP) can be as low as 500 mm/ yr^{-1} near Great Brak River, and as high as 1,200 mm/ yr^{-1} at Jonkersberg, Diepwalle and Storms River (Geldenhuys, 1991). In comparison, the lower and upper climatic limits of fynbos distribution in the southern Cape are MAP 310 and 1120 mm/yr^{-1}, respectively (Rebelo, et al. 2006). The southern Cape forests also often transition to fynbos where there is little or no difference in climate or substrate (Phillips, 1930; Adamson, 1953; Mucina and Geldenhuys, 2006; Keeley, et al. 2012; Allsop, et al. 2014). Other factors must therefore be invoked to explain the distribution of fynbos and forest in the southern Cape.

Both the structural and chemical characteristics of fynbos promote fire, and the same set of properties appear to retard fire in afromontane forest. Fynbos is characterised by a near continuous litter layer with abundant graminoids, short and medium sized shrubs, and small tree and medium sized trees, in varying combinations. This results

in close coupling of biomass compartments, resulting in stand-destroying crown fires. The adjacent forests have a discontinuous understory with few graminoids, and display pronounced separation between the litter layer, understory and the canopy (Keeley, et al. 2012). Chemical properties seem to be less important. van Wilgen, et al. (1992) found that heat yields from combusted fynbos were only marginally higher than for afromontane forest species (21,900 J g^{-1} and 20,700 J g^{-1} respectively). This is relatively low in forest species (3%). These factors combined, fynbos is highly flammable, and forest is not.

Geldenhuys (1994) argues that forests persist in orographic refugia where fires are unlikely. He proposes that climate and soils determine the potential distribution of fynbos and forest, but the actual location of forest patches is determined by the pattern of fires in the landscape. The fire pattern is in turn determined by the interactions among prevailing winds and local geomorphology. In late summer, warm, dry air from the arid South African interior is drawn towards low pressure systems moving from west to east across the southern coast (Tyson, 1964). In combination with lightning, these weather systems promote fire in fynbos. Afrotemperate forest islands persist in fire-free refugia formed in troughs on the lee side of in abutting mountains to the north, or in steep sided gorges where aridity stress is lower than surrounding areas. Areas without orographic protection from these winds are subject to more frequent fire than those in sheltered refugia (Figure 2.17, 2.18).

Fynbos is distributed on strongly oligotrophic soils, and forest soils are generally better developed and more nutrient rich (Cowling, 1995). The suggestion of nutrients as a limiting factor at the ecotone however has been undermined because whole forest patches in the southern Cape can be observed to transcend shale/ sandstone substrate boundaries (Geldenhuys 1994). Bond (2010) demonstrates that most fynbos soils have sufficient micronutrient stock to accommodate forest when soils are deep enough to allow development of deep root systems. Similarly, van Daalen (1981) demonstrated that forest can establish on almost any soils in the southern Cape, and that fynbos and forest soils rarely differ substantially. When differences do occur between soil nutrient content in the respective habitats, van Daalen suggests that these differences

are attributable to the vegetation itself following establishment, rather than being a driver of initial vegetation change.

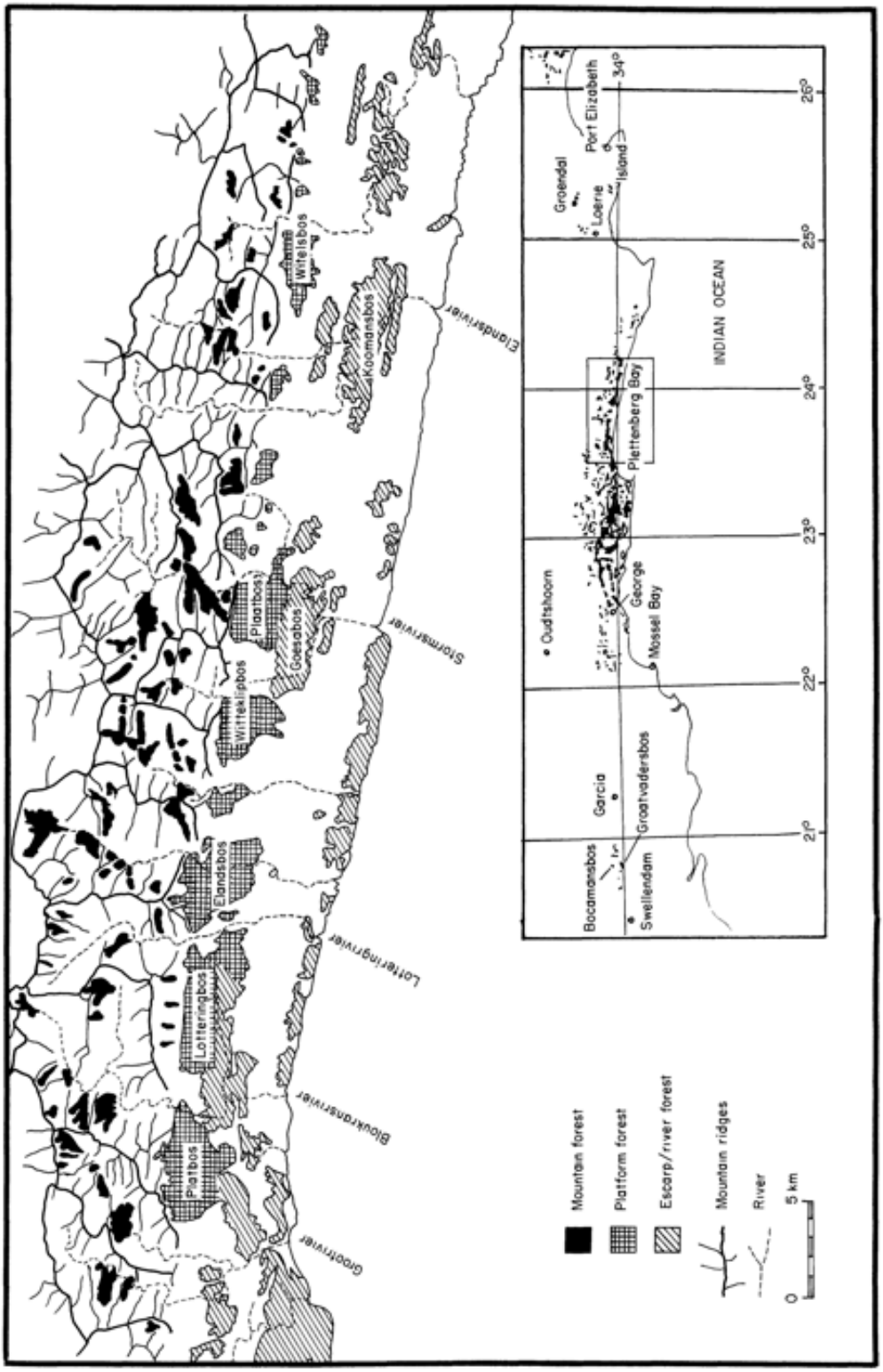

Figure 2.17. The location and pattern of the southern Cape forests in the Tsitsikama area. (Geldenhuys, 1994)

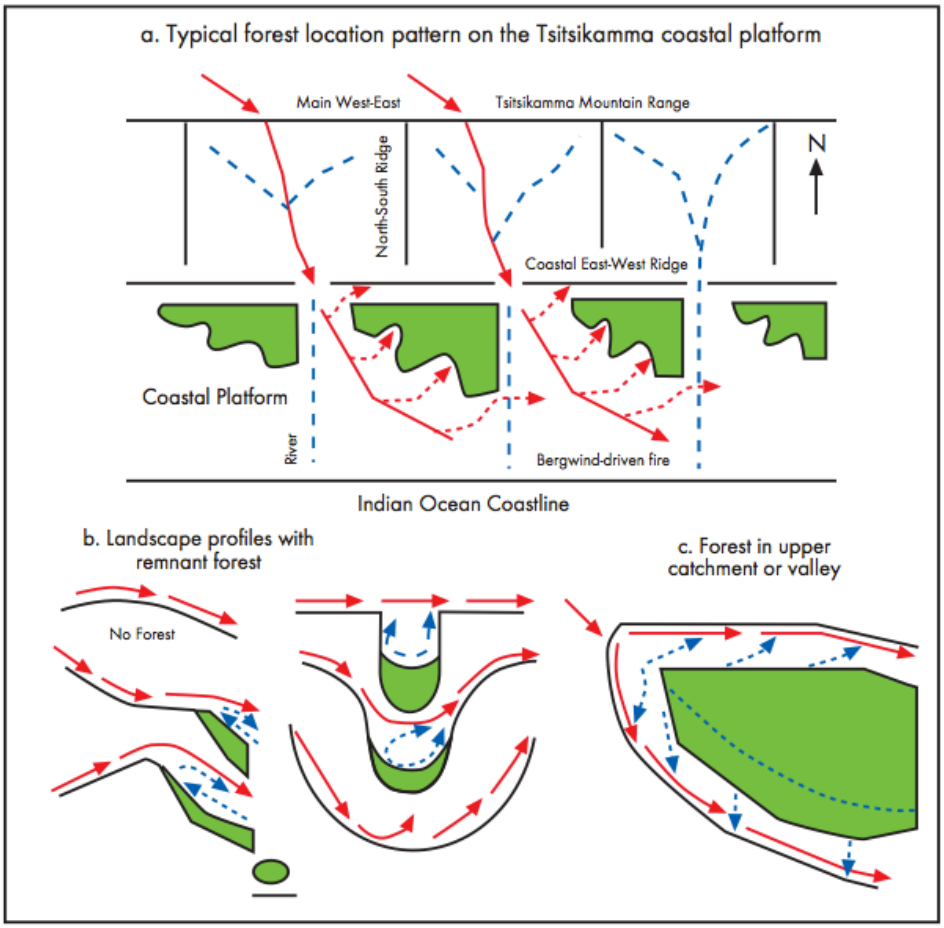

Figure 2.18. Schematic representation of air flow in response to topographic barriers and southern Cape forest distribution in wind and fire shadow areas (from Mucina and Geldenhuys, 2006, adapted from Geldenhuys, 1994).

The boundary between fynbos and forest is often interrupted by a transitional zone dominated by the legume *Virgilia divaricata* and/ or *V. oroboides* (Figure 2.19) (Adamson, 1938; Phillips, 1926). Other species characteristic of this zone include Rhus spp. and a number of members of Celastraceae including species of Maytenus, Pterocelastrus and Cassine. These species have been suggested as forest expansion pioneers, their increased abundance at forest margins being an apparent precursor to woody expansion. The establishment of such species may lead to modification of the microenvironment by providing shade, reducing moisture stress and hence facilitating establishment of forest seedlings that might otherwise be susceptible to xylem cavitation during establishment (Coetsee, et al. 2013; Coetsee, et al. 2015). However, high fire frequencies in fynbos are likely to kill saplings of pioneer taxa, precluding their establishment (Midgley, et al. 1997).

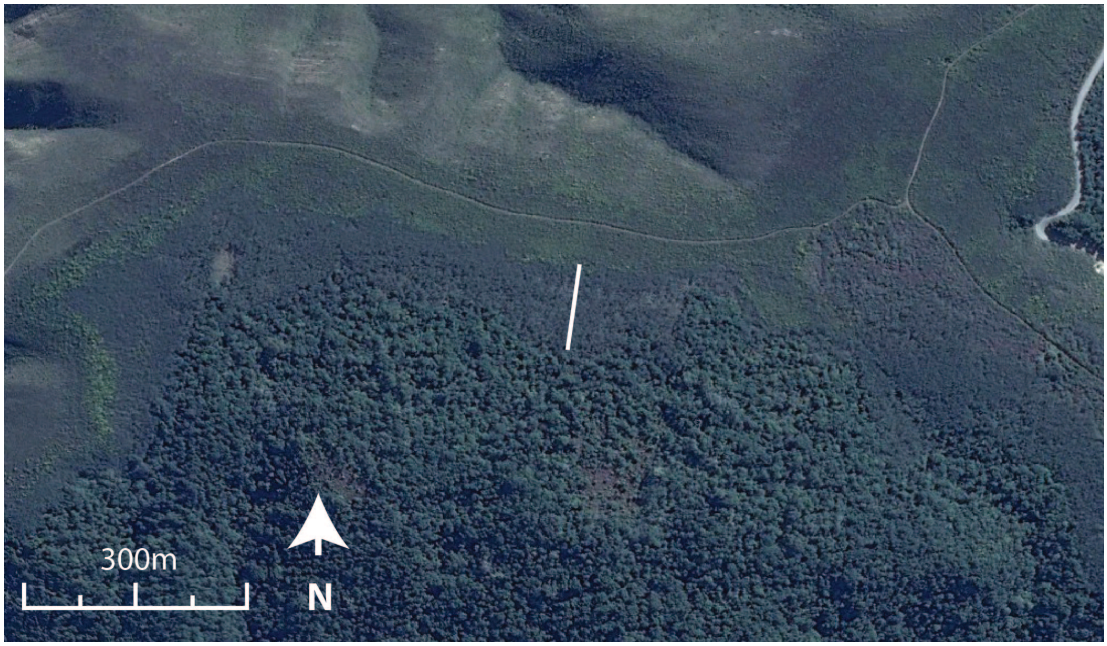

Figure 2.19. Satellite image of the fynbos-afrotemperate ecotone north of Natures Valley. The white line identified the transitional edge zone dominated by Virgilia *spp.*

Coetsee, et al. (2015) proposed that *V. divaricata* facilitates forest development through rapid establishment in the immediate post-fire phase at forest boundaries. Nitrogen fixation and rapid growth of this pioneer species could provide superfluous nutrients for luxuriant growth of arboreal taxa in the immediate post-fire phase. Rapid growth could allow forest-edge trees to mature past the seedling stage and develop fire resistant properties before the next burn occurs in fynbos. This process, in combination with increased habitat for shade-loving forest species, could facilitate secondary forest growth. Coetsee and Wigley tested this hypothesis by conducting soil nutrient gradient analyses across fynbos/ forest ecotones in the Nature's Valley area. Sites dominated by fynbos, *V. divaricata* and afrotemperate forest, respectively, emerged as consistently identifiable along a gradient of increasing fertility. Their findings indicate that *V. divaricata* can enhance soil fertility at the fynbos/ forest boundary and may facilitate shifts between alternative stable states.

Coetsee, et al. (2015) suggest that it may be useful to interpret fynbos-afrotemperate forest dynamics with reference to process models developed at forest-savanna transitions. Hoffman, et al. (2012) highlight how interactions among climate, resources and plant traits determine the distributions of savanna and forest in central

Brazil. Two critical thresholds were identified that determine these interactions. The 'fire resistance' threshold is reached when individual trees develop sufficient bark to insulate the living stem from heat during fire events, preventing death and promoting persistence of individual trees. In contrast, the 'fire suppression' threshold is reached when tree canopy cover is sufficient to shade-out grasses which inhibits fire. This subsequently allows establishment of fire sensitive secondary or tertiary forest taxa. For forests and forest species to surpass these thresholds, long fire-free intervals are required. Hoffmann, et al. suggest that biome switches are more common at sites where resources such as moisture and nutrients are abundant than relatively impoverished sites corresponding to the of time taken to surpass these respective thresholds.

Scheffer, et al. (2014) argued that global scale trait data (Kattge, et al. 2011) show a bifurcation in the maximum height of woody plants. Frequency distributions indicate modal maximum heights of around 2.5 and 25 m, which represent shrubs and trees, respectively, but an apparent scarcity of trees 8-10 m. The latter group of intermediate heights have been termed 'trubs', and their absence is indicative of the factors determining the boundary between shrubs and forests. Shrubs tend to be very well adapted to disturbance. For example, they generally re-sprout easily, and spread the resource cost of damage by having many stems. Trees, in contrast, escape disturbance by growing tall quickly at a relatively low carbon cost. The authors suggest that the intermediate form may be evolutionarily sub-optimal. Such biotic processes account for the stark contrast in vegetation structure visible at the fynbos afrotemperate forest ecotone. This observation is consistent with the mechanistic process for forest expansion proposed by Coetsee, et al. (2015), whereby afrotemperate forests increase soil nutrients resulting in faster growth rates and escape from fire. Indeed, the present spatial distribution can, by eye at least, be observed to support the trubs hypothesis of Scheffer, et al. (2014). The dominant cover of woody plants on the southern Cape plateau is of high canopy afrotemperate trees and fynbos shrubs, with only a narrow band of intermediate height trees at the ecotone (Figure 2.19) (Phillips 1926, 1930). It thus may represent a microcosm of the global nature of vegetation distributions. Coetsee, et al. (2015) suggest the application of savanna-grassland models in understanding the fynbos-afrotemperate forest ecotone. Indeed, palaeoecological data

from these systems has been shown to reveal regime shifts (e.g. Gillson and Ekblom, 2009).

This observation has sparked significant debate, with a number of authors providing both opposing (McGlone, et al. 2015; Qian, 2015; Qian and Ricklefs, 2015) and supporting analyses (Larjavaara, 2015; Scheffer, et al. 2015; Xu, et al. 2015), which have largely focused on the statistical methods and are therefore not discussed further here. However, the reaction evident in the response of McGlone, et al (2015 pp. 4) is certainly telling of the underlying theme:

> "While the world may appear to be sharply divided into 'alternative stable landscape states', the reality is that environmental variation is continuous, and the distribution of woody plant heights reflects this."

Clearly, the Clementsian/ Gleasonian debates in community ecology wage on and, in this case, biome distribution in the southern Cape represents a microcosm of this. Yet in the palaeoecological literature the prevailing view is that these controversial debates have been reviewed amply (Jackson and Blois 2015). Exclusion of such fundamental debates from palaeoecological may result in further perceived incompatibility between neo-ecology and palaeoecology (Froyd and Willis 2007). Efforts should be made to acknowledge and address such debates in order to further the development of the field of applied palaeoecology.

2.6. PALAEOENVIRONMENTS OF THE GREATER CAPE FLORISTIC REGION

Southern Africa's climate is positioned at the geographical interface between tropical and temperate systems. It is subject to the influence of the Intertropical Convergence Zone, the westerlies, and the development and position of continental and oceanic high pressure systems and, as such, experiences varying degrees of winter and summer rainfall (Figure 2.21). During the Holocene substantial changes in precipitation amount and seasonality occurred across the subcontinent and have been linked to the relative dominance of these dynamic climate systems (Chase, et al.

2013). Key to understanding this discussion has been the extent to which heuristic models (e.g. Cockroft et al. 1987) that link the region's climatic history to propagation of Antarctic sea-ice leading to equatorward migrations of the westerlies, more frequent/intense winter storms and northerly and eastward expansion of the Winter Rainfall Zone (WRZ) (Figure 2.21) (Chase and Meadows, 2007).

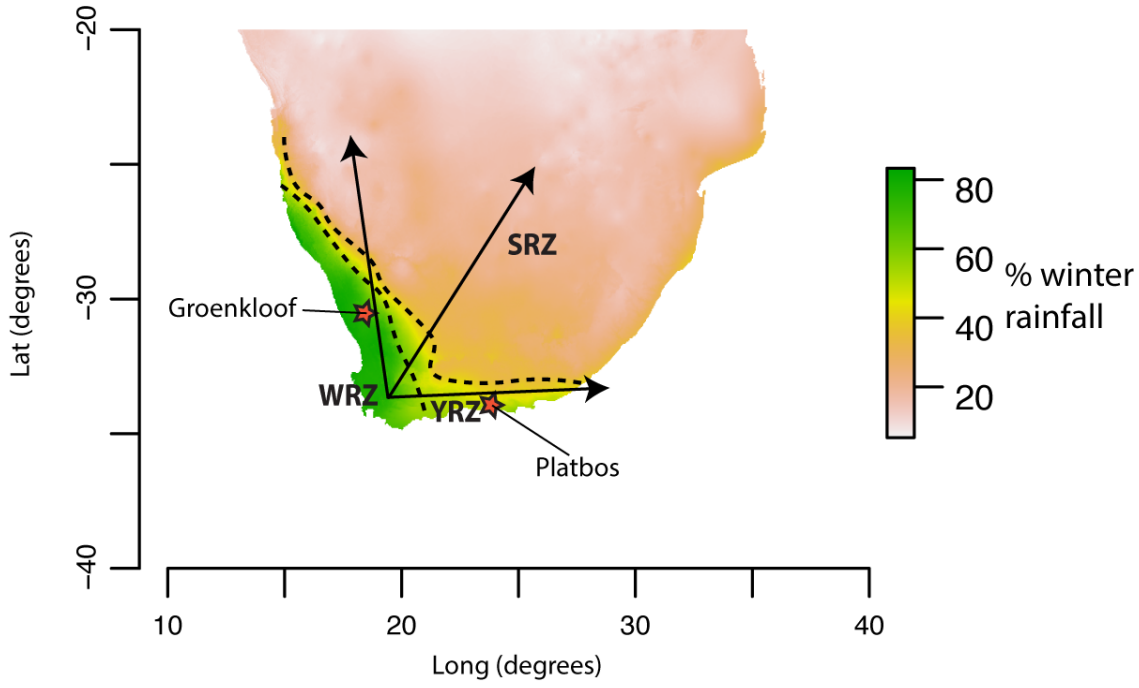

Figure 2.21. Winter rainfall zone of southern Africa. Arrows indicate the direction of expansion during cold phases resulting from interaction among Antarctic sea-ice and the westerlies.

2.6.1. The Mid-Holocene Altithermal (8,000-4,000 cal yrs BP)

The Mid-Holocene Altithermal (MHA) is a globally recognised temperature maximum within the current geological epoch (11,000-10,000 cal yrs BP to present). The MHA is expressed in southern Africa between 8,000-4,000 cal yrs BP (Chase and Meadows, 2007), though with sub-regional variability in timing and magnitude. At Uitenhage in the southwest Eastern Cape of South Africa temperatures between 7,000-4,500 years cal BP may have been as much as 2-3^{o}C warmer that present day conditions (Heaton, et al. 1983), and maximum warming of 1^{o}C above present is recorded at Stampriet in east-central Namibia between 10,000 and 6,000 years cal BP (Figure 3.22) (Stute and Talma, 1997). At Bloomplaas and Wonderkrater in north eastern South Africa maximum Holocene temperatures were reached at 7,000-4,500

cal yrs BP (Scott and Thackeray, 1987; Thackeray, 1990). The MHA is thus geographically variable in magnitude, but is a persistent feature in southern African palaeotemperature records.

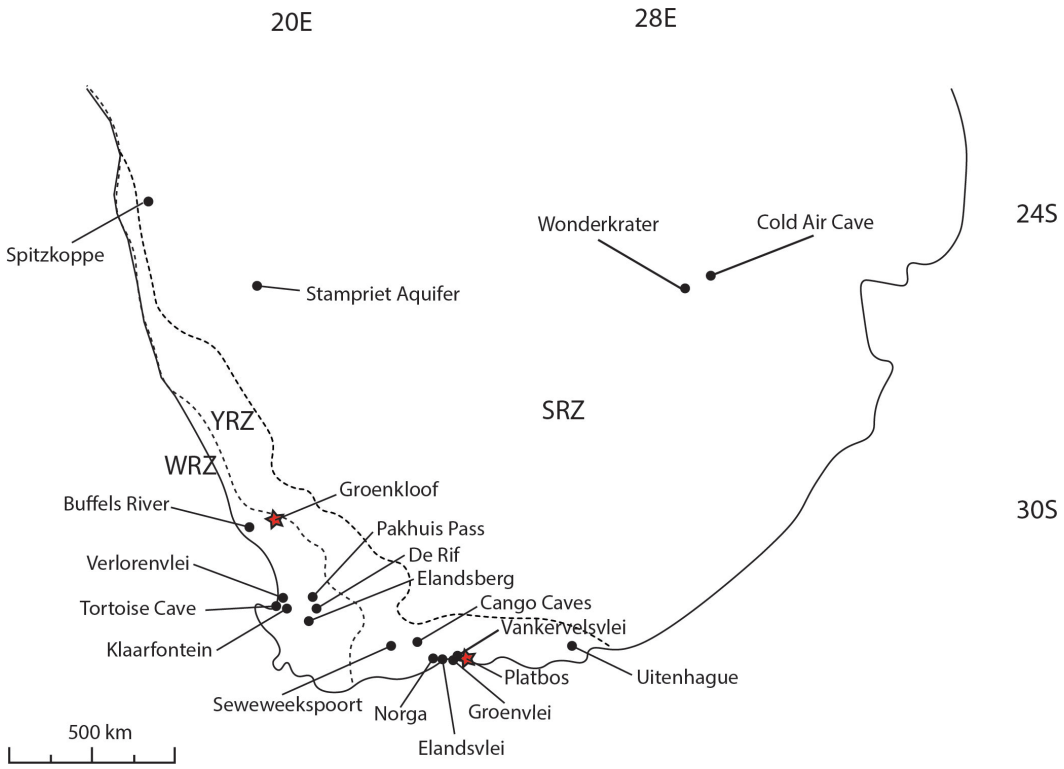

Figure 2.22. Location map of key palaeoenvironmental sites mentioned in the text.

Determining the impact of palaeotemperature gradients on moisture availability has until recently relied predominantly on fossil pollen and charcoal as climate proxies (Chase and Meadows, 2007). Fossil charcoal fragments of mesophytic thicket taxa from Elands Bay Cave begin to decline in abundance at the beginning of the Holocene epoch, and are absent by 4,700 cal yrs BP (Parkington, et al., 2000). A comparable trend is reflected in the pollen record from Klaarfontein Springs, some 18 km inland from Elands Bay Cave (Meadows and Baxter, 2001). Between 7,000 BP to 4,000 cal yrs BP the pollen spectra are dominated by Poaceae, Asteraceae and Chenopodiaceae, likely reflecting an environment that is more arid than present. Pollen data from a nearby estuary at Verlorenvlei in Elands Bay suggest that the observed trends at Klaarfontein Springs were geographically coherent (Meadows, et al. 1996), with higher proportions of Poaceae and Mesembreanthemaceae

(Mesembreanthemoidiae) pollen from 6,300-4,500 yrs BP. Further evidence of climatic change along the south western coastal margin of South Africa is provided by (Chase and Thomas, 2006, 2007). Increased dune formation during the period 8,000-4000 yrs BP is interpreted as a proxy for enhanced aeolian activity resulting from decreased rainfall and hence lower vegetation cover (Chase and Thomas, 2006, 2007); however the clarity of this trend is spatially and temporally disharmonious.

Chase, et al. (2013) analysed two rock hyrax middens from the year-round rainfall zone of the southern Cape at Seweweekspoort (Figure 2.23). The authors compare stable nitrogen and carbon isotope data from these middens with a record of relative temperature change from the nearby Cango Cave speleothem deposits (Talma and Vogel, 1992) and infer a negative relationship between temperature and humidity at the site. By stratigraphic correlation with proxies for sea-surface temperatures, and southern hemisphere westerlies circulation intensity (Cohen and Tyson, 1995; Lamy, et al. 2001; Fischer, et al. 2005), Chase, et al. demonstrate a mechanistic relationship between Antarctic sea-ice extent and the strength and position of the westerlies. The most prominent trend in the record occurs between 7,000-5,000 cal yrs BP when a reduction in sea-ice extent corresponds to a southward shift in the westerlies and pronounced aridity under increased temperatures. This relationship is less clear in the latter Holocene. Nevertheless, this record provides strong support for heuristic models such as those of Cockroft, et al. (1987) and Cohen and Tyson (1995) (Figure 2.24), and increased aridity in the south western Cape during the MHA therefore likely resulted from a poleward contraction of the rainfall zone and increased influence of the South Atlantic Anticyclone (SAA).

Palaeoenvironmental conditions in Namibia during the early to mid-Holocene are polarised with those of the south and south western Cape. While records from the south manifest indications of a dryer MHA, records from central and west Namibia indicate more mesic conditions. Stable carbon and nitrogen isotope analysis of hyrax middens at Spitzkoppe and Austerlitz indicate progressive aridification through the Holocene, conditions being generally more mesic between 8,700-3,500 cal yrs BP than in the late-Holocene (Chase, et al, 2009, 2010). Records of increased air from the Stampriet Aquifer between 13,000-5,000 cal yr BP (Stute and Talma, 1998), and

pollen indicative of increased rainfall between 7,800-6,800 from spring deposits in Windhoek (Scott, et al. 1994), corroborate interpretation of Chase, et al. (2009, 2010) that higher than present humidity prevailed at Sitzkoppe and Austerlitz.

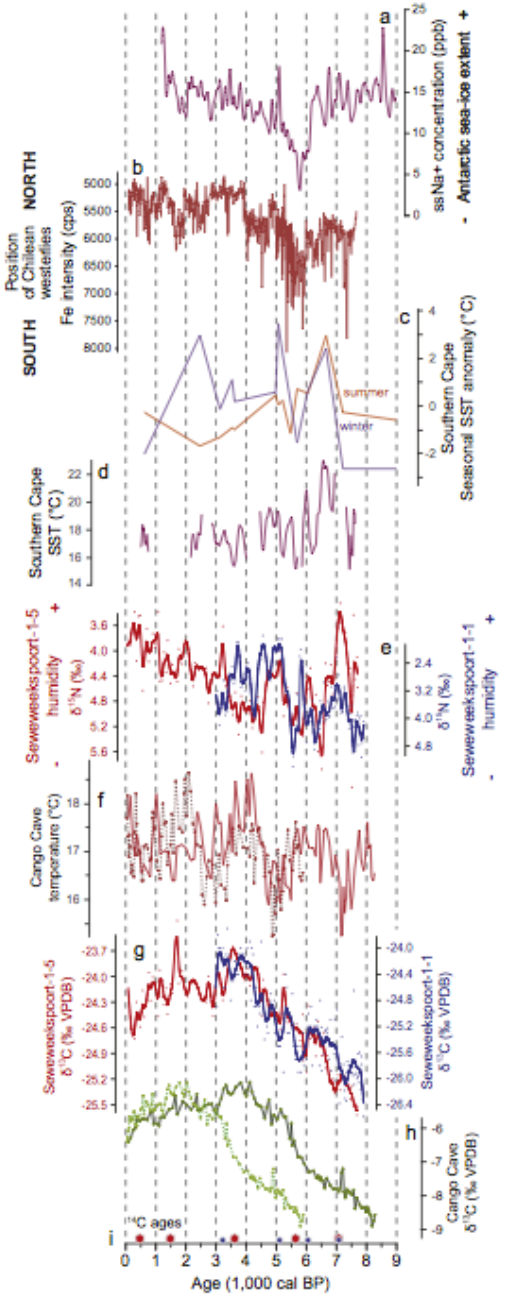

Figure 2.23. Comparison of d^{15}N (e) and d^{13}C values (g) for the Seweweekspoort-1-1 and Seweweekspoort-1-5 hyrax middens with relevant regional palaeoenvironmental records. Sea-surface temperature (SST) (d) and seasonal SST anomaly records (c) derived from stable isotope analyses of shells from Nelson Bay Cave (Cohen and Tyson, 1995), and d^{13}C (h) and palaeotemperature (f) reconstructions from a speleothem from Cango Cave (Talma and Vogel, 1992), iron concentrations

from the Chilean continental margin at 41S (b; Lamy et al., 2001) and sea salt sodium concentrations from the EPICA DML ice core in Antarctica (a; Fischer et al., 2007).

A strong positive correlation exists between $\delta^{15}N$ values and the intensity of the Benguela Upwelling System (BUS) at Sitzkoppe and Austerlitz (Chase, et al., 2009, 2011) (Figure 2.25). Less positive $\delta^{15}N$ values indicate that more humid conditions correspond to decreased BUS intensity during the MHA. Low BUS upwelling intensity likely resulted from a decrease in the strength of the South Atlantic Anticyclone (SAA) and a southerly shift in its position (Nicolson, 2000). Applying heuristic models such as those of Cockroft, et al. (1987) this resulted from a poleward retreat of the westerlies and Antarctic sea-ice under warmer temperatures of the MHA. Therefore, in contrast to records of increased aridity in the south western Cape, greater humidity in Namibia in the mid-Holocene was likely a result of increased easterly flow and summer rainfall advective systems under warmer temperatures (Eitel, et al. 2002; Chase and Meadows, 2007) and a less dominant influence of the SAA.

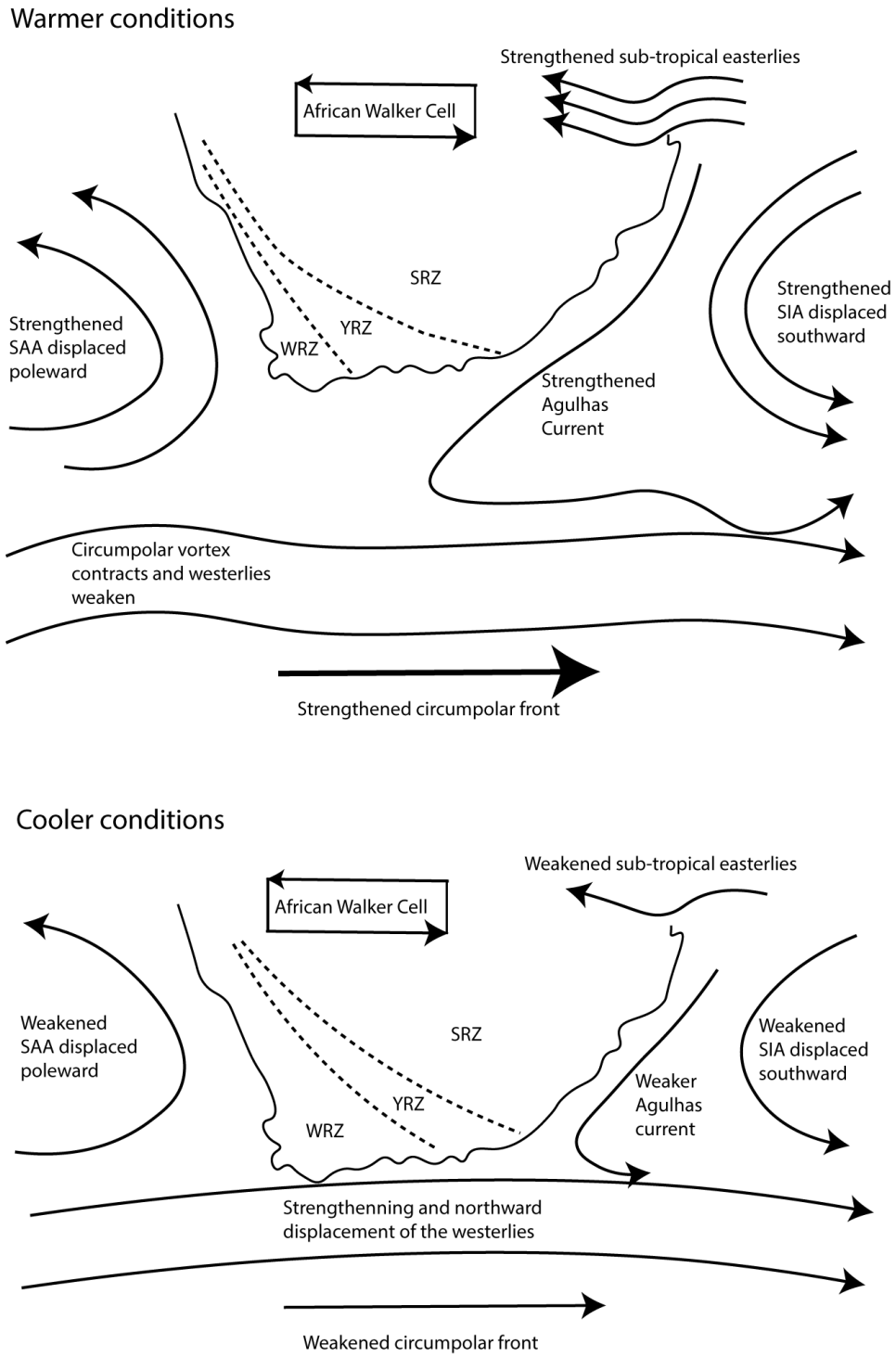

Figure 2.24. Conceptual diagram describing the strength and position of the southern African circulation systems under relatively warm (top) and cool (below). Not the position of the winter rainfall zone (WRZ), year-round rainfall zone (YRZ), summer rainfall zone, the South Atlantic Anticyclone (SAA) and the westerlies. Figure adapted from Cohen and Tyson (1995) in Kirsten (2013).

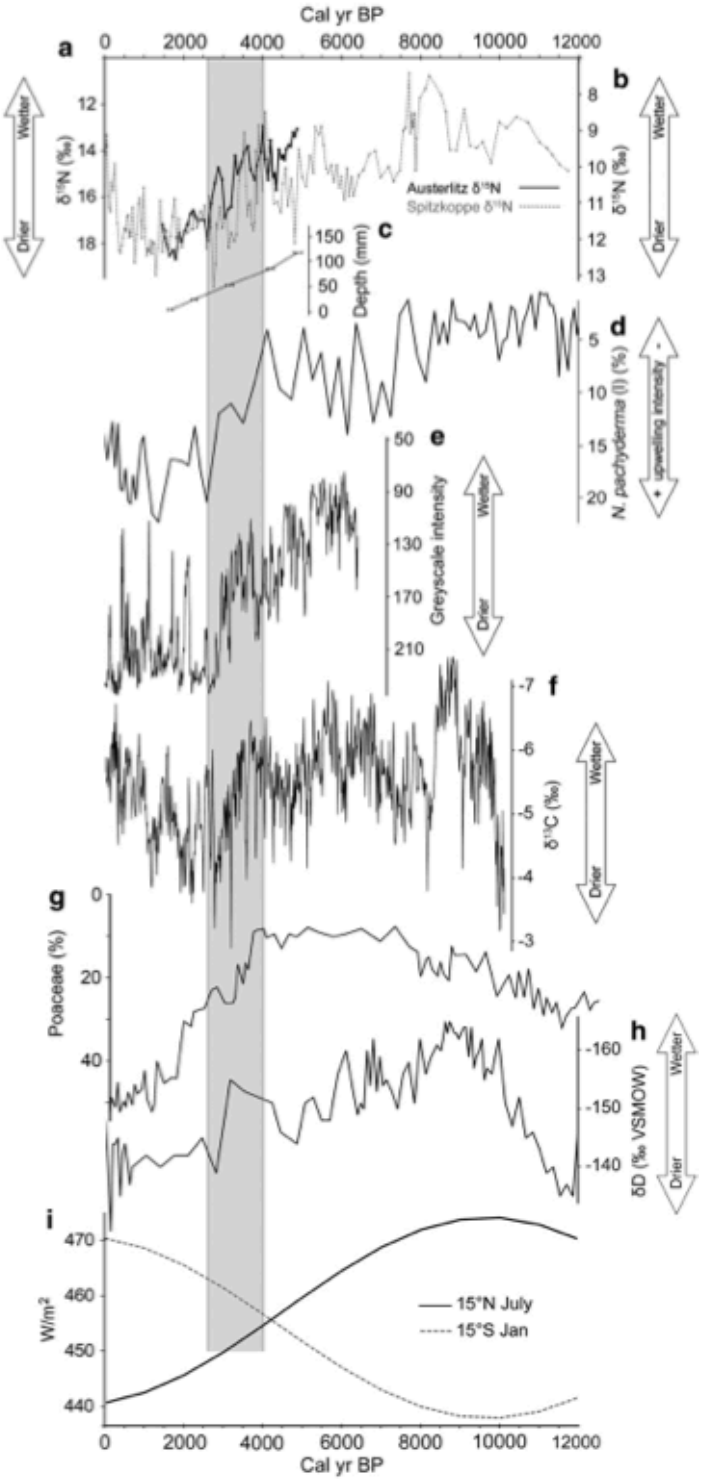

Figure 2.25. Comparison of $\delta^{15}N$ records from the Austerlitz hyrax midden (a) with $\delta^{15}N$ records from the Spitzkoppe hyrax middens (b) (Chase et al., 2009); N. pachyderma percentages from the Benguela upwelling region (d) (Farmer et al., 2005), Cold Air Cave speleothem grey scale measurements (e) (Lee-Thorp et al., 2001), Cold Air Cave speleothem $\delta^{13}C$ values (f) (Holmgren et al., 2003), the percentage of grass pollen at ODP Site 1078 off the coast of central Angola (g) (DuPont et al., 2008), δD values from plant waxes in marine core GeoB 6518-1 off the Congo River mouth (h) (Schefuß et al., 2005), and summer insolation at 15°N and 15°S (i) (Berger and Loutre, 1991). Figure and text from Chase, et al. (2010).

2.6.2. The Southern African Neoglacial Phase (4,000-2,000 cal yrs BP)

Palaeotemperature records for the period 4,000-2000 cal yrs BP are particularly sparse. Between 4,000-2,000 yrs BP a cooling is evident at both Stampriet and Uitenhage of magnitudes 0.5^{o}C and 3^{o}C, respectively. The Cango Cave Speleothem temperature record shows a negative departure from the MHA by as much 2.5^{o}C It can therefore be hypothesised, under the assumptions of the prevailing conceptual climate models (Chase and Meadows, 2007), that the inverse climatic and biogeographical polarisation observed during the warm MHA should be evidenced in palaeoenvironmental records during this time. In other words, the south western and southern Cape should experience more mesic conditions as the westerlies propagate northwards in response to expanding sea ice, whereas humidity in sub-tropical Namibia should decrease as the SAA propagates northward, enhancing BUS intensity and blocking moisture-bearing easterly summer rainfall systems (Figure 2.26).

Palaeoecological data from the south western Cape supports this hypothesis. Pollen and spores from Klaarfontein Springs show reductions of xerophytic taxa such as Chenopodiaceae and Mesembreanthemaceae and an increase in the abundance of riparian types such as Typha, Juncus and Cyperaceae between 4,000-2,000 cal yrs BP. These data are interpreted as indicating increased moisture availability between 4,000-2,000 cal yrs BP (Meadows and Baxter, 2001) as a result of greater influences of the westerlies following termination of the MHA (Chase and Meadows, 2007). As during the MHA, interpretation of the regional trends can tentatively be drawn from the records at Cango Caves (Talma and Vogel, 1992) and Seweweekspoort (Chase, et al. 2013). Inferred temperature reductions compared to the MHA maximum are as great as -2.5^{o}C during the period 4,000-2,000 cal yrs BP.

2.6.3. Environmental Change in the Past Two Millennia (2,000 cal yrs BP to near present)

Sub-continental similarities suggest that temperature changes have been coherent over fairly large geographical scales for the past two millennia (Nicholson, et al. 2013; Weldeab, et al. 2013; Zhao, et al 2016). Globally recognised climatic events in the late Holocene such as the Medieval Climate Anomaly (MCA, 1,000-700 cal yrs BP/

AD 950-1,250) and the Little Ice Age (LIA, 650-100 cal yrs BP/ AD 1,300-1850) have been identified in the region (e.g. Tyson and Lyndesay, 1992) but are much less pronounced than the MHA. Stager et al. (2012) produced a palaeohydrological records from geochemical and diatom analysis of sediments at Verlorenvlei on the west coast of South Africa. They hypothesised, based on the heuristic models outlined above, that LIA cooling would be accompanied by increased winter-rainfall inputs. Freshwater inputs rose notably through the LIA, with notable pulses around c. 600, 530, 470, 330, 200, 90 and 20 cal yrs BP. Benito, et al. (2011) similarly identified the LIA as being characterised on the west coast of South Africa by a strongly positive hydrological and attributed this to enhanced winter rainfall. Further, Weledeab, et al (2013) suggest that the LIA was likely the wettest part of the Holocene in the winter-rainfall zone.

2.6.4. Land-use Change in the Cape Floristic Region

Interpretations of the timing and nature of land-use changes in southern Africa are subject to much ongoing debate. Intensification from low impact hunter gatherers of the Khoi San to partially intensive herding occurred as early as 2000 cal yrs BP in the western portion of South Africa. On the west coast of South Africa at Klaarfontein Springs, south of Lamberts Bay, pollen analysis of lake sediments suggests two phases of agricultural intensification during the late-Holocene (Meadows and Baxter 2001). These are evidenced by increases in the abundance of disturbance indicators, and reductions in fire sensitive taxa and grasses. Initiation of these trends occurs at around 2,000 yrs BP and is linked by the authors to the arrival of Khoi Khoi pastoralists in the region. A second phase of much higher intensity land use is concurrent with the expansion of colonial European agriculture at the Cape at around AD 1700. Arrival of herders in the southern Cape is likely to have been later likely reflecting differential migration patterns (Sadr, 2015). Archaeological evidence from Bloomplaas Cave in the Still Baai area of the southern Cape suggest that initial sedentary herding occurred somewhat earlier around AD 390-475 (1550-1475 cal yrs BP) (Damm and Hagedorn, 2010; Deacon, 1995).

2.6.5. Palaeoecological Evidence of Fynbos Resilience

The Cederberg mountain range, situated inland to the east of Eland's Bay, has been an important focus of palaeoenvironmental research in southern Africa (Chase and Meadows, 2007). A recent study has documented overturning between differing fynbos types (say which ones) in response to climatic change in high-altitude mountain fynbos using fossil pollen, charcoal and stable isotope data from a hyrax midden from DeRif (Figure 2.26) (Valsecchi, et al. 2013). The high temporal resolution of this record has revealed a dynamic fynbos system with overturning among fynbos taxa including members of Proteaceae, Restionaceae and Asteraceae. Despite high overturning within-biome, this largely confirms previous fossil pollen studies in the area that suggest the Cederberg mountain fynbos has remained resilient at the between-biome scale since the Last Glacial Maximum (LGM) (Meadows and Sugden, 1991, 1993; Meadows, et al. 2010; Quick, et al. 2013). The resilience of Cederberg mountain fynbos through the Holocene has been attributed to a climatic buffering effect associated with orographic rainfall, and strong substrate association of fynbos and succulent karoo (Meadows et al 2010; Quick, et al. 2011; Valsecchi, et al. 2013).

Scott and Woodborne (2007a, b) found a strong representation of karroid taxa in their hyrax midden pollen record from Pukhuis Pass in the Central Cederberg through the Holocene, including variable abundances of Pentzia-type, Aizoaceae and Scrophulariaceae-type, but also abundant fynbos elements such as Restionaceae. The greater representation of karroid taxa at Pukhuis Pass compared to DeRif has been attributed to the position of the former closer to the biome boundary and large areas of succulent karoo (Quick, et al, 2011; Valsecchi, et al., 2013). Interestingly, increased prevalence of the karroid taxa occurs at the Last Glacial-Interglacial Transition where aridity is known to have increased significantly in the Cederberg area (Chase and Meadows, 2007; Scott and Woodborne, 2007a, b; Quick, et al. 2011; Valsecchi, et al. 2013), suggesting a biome shift potentially occurred. However charcoal data is unavailable for the Pukhuis Pass record, and temporal resolution is coarse, which impedes analysis of long-term relationships between fynbos, succulent karoo and fire.

Palaeoecological data pertaining to the fynbos-afromontane forest boundary are perhaps more scarce still. Martin (1968) produced two pollen records from Groenvlei in the southern Cape, within the Wilderness Embayment lakes and close to Natures Valley. During the earliest portion of the record from around 8,000 14C yrs BP fluctuation between dry fynbos and forest elements that likely extended onto dunes in the area. Scholtz (1986) similarly recorded significant fluctuations between fynbos and forest pollen in the southern Cape during the Holocene, though both assumed that climate has been the dominant parameter controlling forest distribution and potentially overlooked the role of fire. More recently, Quick et al. (2015) produced pollen, charcoal sedimentological data from Vankervelsvlei again located in the southern Cape fynbos-forest complex from close to a sharp biome transition. A chronology was constructed using optically stimulated luminescence and radiocarbon dating for the past 140,000 years, which incorporates the Last Interglacial phase (LIG). Warmer conditions than present in the LIG corresponded to enhanced forest distribution as well as during subsequent cold glacial conditions. The authors hypothesise this is a result of reduced aridity stress under warmer conditions as a result of enhanced easterly flow during summer.

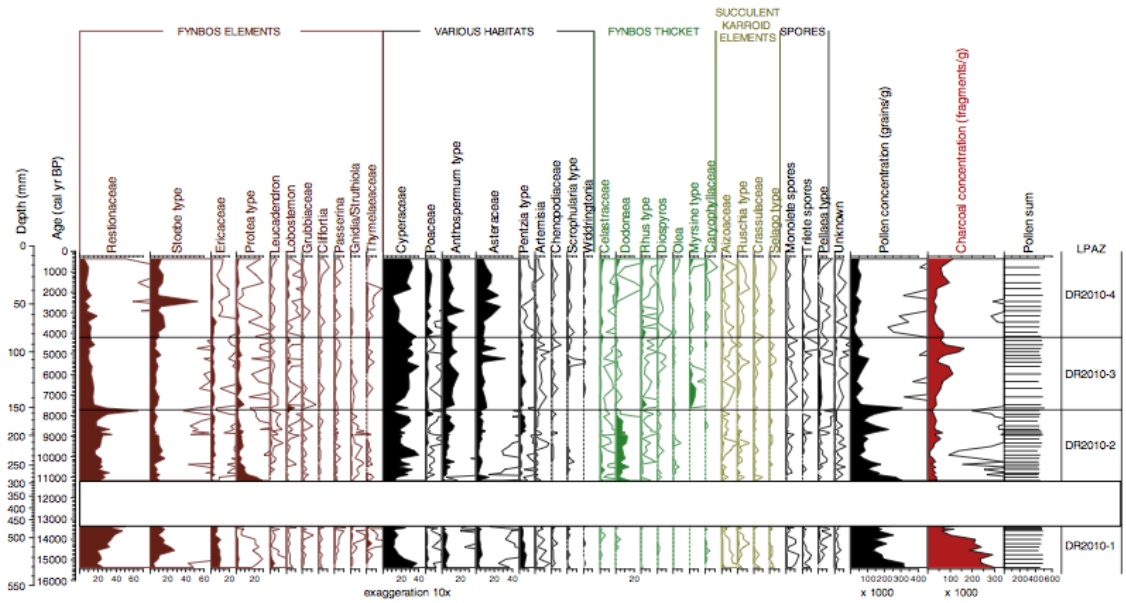

Figure 2.26. Percentage pollen and microcharcoal concentration diagram for section DR2010 at De Rif (Valsecchi, et al. 2013).

Reasons for the apparent paucity of palaeoecological data at fynbos boundaries include difficulties locating suitable microfossil archives close to biome boundaries (Chase and Meadows, 2007); a general propensity for Quaternary scientists to give preference to sites with greater temporal extension and quality proxies rather than high temporal resolution needed for studying ecological changes (Froyd and Willis, 2008); a lack of studies from the region that provide charcoal proxy data (e.g. Meadows and Baxter, 2001; Scott and Woodborne, 2007). Although Quick, et al. (2011) enumerate charcoal data at the DeRif midden in the Cederberg, coarse temporal resolution make interpretations of the impact of fire on Fynbos problematic. While Valsecchi, et al. (2013), from the same midden, provide charcoal analytic data, the site is far from the ecotone (c. 40 km) and so is not ideally suited for analysis of biome boundary dynamics (at least in the region, where Quaternary environmental changes have been mute relative to other regions).

2.7. SUMMARY OF LITERATURE REVIEW

Palaeoecology offers great potential to test theory developed within contemporary ecology, in particular resilience and alternative stable states theories (DeBoer, et al. 2013; Gillson and Ekblom, 2009; Gil-Romera, et al. 2013; Holling, 1973; Holling, et al. 2002; Oliver, et al. 2015; Quick, et al. 2011; Scheffer, et al. 2001; Valsecchi, et al. 2013). It also offers a valuable vehicle with which to explore fundamental concepts regarding the nature of ecosystem organisation (Blois, et al. 2015; Darwin, 1859; Louthan, et al. 2015; Schimper, 1903; MacArthur, 1972; Jackson 2006; Williams and Jackson, 2004). These applications are particularly pertinent in the face of present and future global environmental changes and the incredible biodiversity held within Mediterranean-type ecosystems. In the Greater Cape Floristic Region there is a need to develop palaeoecological records that are near biome boundaries (see Chase and Meadows, 2007), where species are particularly sensitive to environmental and ecological change (Agenbag, et al. 2008; Esler, et al. 2015; Quick, et al. 2015). Palaeoecologists can maximise the ecological information derived from their studies by focussing on high resolution multi-proxy studies at biome boundaries – in particular, where physiological and biotic boundaries can be compared. Further, there is a need to interpret such records within strong theoretical ecological frameworks,

rather than solely palaeoclimatic/ palaeoenvironmental investigations (Froyd and Willis, 2008; Slingsby, et al. 2014).

3. STUDY AREA AND METHODS

3.1 REGIONAL BIOME DISTRIBUTION AND CHARACTER

The floristic communities of the Greater Cape Floristic Region are highly diverse owing to high local species richness together with high species turnover along environmental and geographical gradients (Mucina and Rutherford, 2006). Numerous attempts have been made to classify the region's flora based on phytogeography (Campbell, et al. 1981; Goldblatt, 1978; Weimarck, 1941) as well as ecological criteria including climate and soils (Acocks, 1953; Rutherford and Westfall, 1986). For the purpose of this study it is essential to explicitly define the biological entities of the Greater Cape Floristic Region (GCFR). The relevant vegetation types discussed in this study include fynbos, succulent karoo, renosterveld and southern afrotemperate forest. These types, together with southern coastal forest and subtropical thicket together compose the GCFR (Figure 1.2). For this, the present study refers to the most recent comprehensive biological classifications associated with fynbos, succulent karoo, renosterveld afrotemperate forest and the GCFR (Mucina and Rutherford, 2006; Bergh, et al. 2014) in order to create an ecologically meaningful classification system.

Fynbos is perhaps the most prominent of the GCFR biomes, containing the greatest number of species and levels of endemism. It is a low, heathland dominated by microphilous ericoid shrubs and shrublets and leafless graminoids of the Restionaceae and Cyperaceae families. Taller shrubs of the Proteaceae family with broader leaves are also characteristic. Delimitation of the fynbos biome is also strongly influenced geographically by association with the Cape Fold Belt Mountains and associated sandstones (Bergh, et al. 2014; Rebelo, et al. 2006). More isolated patches of fynbos vegetation also occur elsewhere in the GCFR, such as on the upper slopes of the Kamiesberg Mountains to the north eastern region amongst a broader landscape of succulent karoo. True Mediterranean-type climate occurs only in the south-western most portion of the biome, as rainfall becomes progressively aseasonal and arid to the east and north respectively, where the mesic and arid limits of fynbos distribution

occur (Chapters 2.4, 2.5). Throughout its entire distribution fynbos is fire prone and adapted (Keeley, et al. 2012), which is a key determining characteristic of the biome.

Succulent karoo is characterised by succulent shrublands with winter or aseasonal rainfall that border the xeric extremes of fynbos and renosterveld (as well as sub-tropical thicket vegetation). It is associated with the driest conditions in the GCFR resulting in a short, cool growing season. It is structurally, ecologically and floristically distinct from fynbos. The vegetation is structurally uniform, being dominated by a high diversity of dwarf leaf-succulent sub-shrubs of Aizoaceae. Other succulents including *Aloe dichotoma, A. pillansii* (Asphodelaceae) and *Tylecodon piniculatus* (Crassulaceae) form trees and geophytes (particularly of Iridaceae) are also an important feature of the flora (Bergh, et al. 2014; Mucina, et al. 2006). At higher elevations, such as in the Kamiesberg, annuals, in particular of the Asteraceae, produce spectacular floral displays in springtime (Chapter 2.4). These displays are typically, but not exclusively, distributed on ruderal habitats such as agricultural land and roadsides, and as such have been regarded as an anthropogenic phenomenon (Cowling, 1999). Grasses also occur in succulent karoo, but are not particularly diverse nor abundant (Desmet, 2007).

Renosterveld has historically been included in the fynbos biome (Acocks, 1953;) largely based on simplistic structural similarities and climate that are central to the biome concept (Raunkiaer, 1934; Rutherford and Westfall, 1986) (Chapter 2.4). For example, it is dominated by fine-leaved shrubs with a graminoid understory, contains a significant proportion of geophytes, is fire prone an adapted and occupies a similar climate space to fynbos. However, recent authors have argued against inclusion of renosterveld within the fynbos biome based on floristic data, and advocate a more detailed approach that is necessarily complex owing to the high floristic and ecological diversity of renosterveld. Multivariate statistical ordination of regional floristic biogeographic data (Bergh, et al. 2014; Mucina and Rutherford, 2006) identify renosterveld as a distinct group, but also as floristically transitional to fynbos and succulent karoo, as well as sub-tropical thicket.

In this study, it is important to distinguish mountain renosterveld from lowland types (Curtis, 2013). The latter are associated with shales in coastal lowland areas, and possess a distinctive, endemic-rich flora that is indeed indicative that renosterveld warrants consideration as a biome in itself. Mountain renosterveld, in contrast, typically occurs inland and forms a narrow zone between the fynbos and succulent karoo biomes, which grades into its neighbouring biomes at their drier and wetter limits, respectively. It is distinguished from fynbos largely on the basis of the dominance of *Elytropappus rhinocerotis*, the absence of key fynbos families (in particular, Proteaceae and Restionaceae) and predominance of true grasses (Rebelo, et al. 2006). Namaqualand Granite Renosterveld, which is of most relevance to this study, is indicated as having particular succulent karoo affinities (Bergh, et al. 2014). This floristic affinity may well result from the patchy nature of this vegetation unit, where succulents interdigitate amongst in fire-free microhabitats fire-prone shrubland in Namaqualand (Anderson, 2008). Indeed the authors acknowledge limitations associated with the scale of the data used, proposing the study as preliminary. Moreover, transect survey data from the Kamiesberg (Appendix 1) do not show partitioning of taxa indicative of the respective vegetation types, which lends support to the notion that mountain renosterveld is a transitional zone rather than a distinct biome.

Albany thicket has been associated with the fynbos biome in the past but differs substantially in structure, function and floristics (Rebelo, et al. 2006). It is defined by incorporation of a large diversity of growth forms including evergreen, broadleaved, sclerophyllous spiny and/ or succulent shrubs to low trees that form a dense, single-layered vegetation. It borders fynbos in the far east of the GCFR. On more mesic sites it can accommodate forest species, and is also highly sensitive to fire (Bergh, et al. 2014). While not specifically a subject of this study, some of its key species typify the boundary between fynbos and forest.

Forests of the GCFR fall into two categories; the southern afrotemperate forest and the southern coastal forests. This study is concerned with interactions between fynbos and the former type (Chapter 2.5), hereafter referred to as afrotemperate forest. These forests have strong floristic links to tropical Africa, and typically occur in high

altitude regions where the growing season is cool. It is only in the GCFR that afrotemperate forest occurs at sea-level. These are tall forests that occur on south and east facing slopes and in ravines of the Cape Fold Belt between Port Elizabeth and Cape Town, though their greatest extent can be found in the Knysna/ Tsitsikama region along a 250 km coastal strip. The upper canopy is dominated by Podocarpaceae (*Podocarpus* and *Afrocarpus*) and can reach over 40 m in height, though there are multiple layers with low trees, shrubs and herbs. The distribution of these forests is controlled by complex and interacting variables including moisture, light, soil nutrients, and topographic protection from fire (Coetsee, et al. 2015; Geldenhuys, 1994). Southern afrotemperate forests exhibit the lowest similarity to any of the other GCFR units. They are surrounded by fynbos vegetation, and are bordered by a zone of transitional vegetation with forest pioneers such as *Rhus, Maytenus, Kiggelaria* and *Virgilia* (Bergh, 2014; Geldenhuys, 1991).

Colville, et al. (2014) identified hierarchical biogeographic units for South African plants based on species similarities. A clear primary split is evident between the flora of the summer rainfall region in the east and the rest of the country. At this first-order level the winter and aseasonal region form a single biogeographic unit conforming generally to the GCFR. A second-order split subsequently emerges within the GCFR conforming to a) the winter-mesic zone; b) the aseasonal mesic zone; and c) the winter-arid zone. This winter-mesic zone generally conforms to the Mediterranean-type WRZ of the south-western Cape, while the aseasonal mesic zone conforms to the YRZ of the southern Cape. The winter-arid zone approximates Namaqualand. Of these three sub-groupings, the winter-mesic and aseasonal-mesic groups cluster most closely in terms of species similarity. These two groupings share a similar geological substrate being related to the Cape Supergroup Rocks (Colville, et al., 2014). Thus, edaphic filtering might be expected to be less strong at this within-biome scale, as the two types can occur on the same substrate.

3.2. REGIONAL CLIMATE

Chase and Meadows (2007) interpret southern African climates based on the dynamics of three broad climatic zones (Figure 3.2). The winter-rainfall zone (WRZ,

>66 % of MAP falling between April-September) is presently situated in the south western Cape, and stretches north along the west coast South Africa (Figure 3.1). The zone receives rainfall resulting from the westerly frontal systems. To the north and east of the subcontinent, summer rainfall dominates (SRZ, >66% of MAP falling between October-March), and is controlled largely by seasonal interplay between the subtropical anticyclonic systems, such as the South Atlantic Anticyclone, and the sub-tropical easterly advective systems. Summer dominance of the latter promotes enhanced moisture-bearing easterly flows (Tyson and Preston-Whyte, 2000). Separating the WRZ and SRZ is a relatively narrow band of climate space that receives both summer and winter precipitation, being influenced by both the aforementioned zones that is commonly referred to as the year-round rainfall zone (YRZ; Chase and Meadows, 2007).

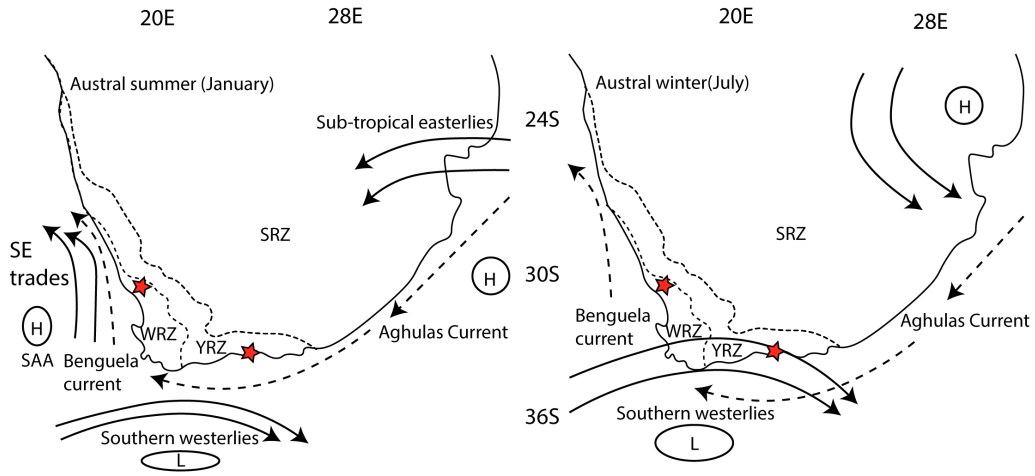

Figure 3.1. Schematic representation of heuristic southern African climate mechanisms. WRZ: Winter rainfall zone; YRZ: Year-round rainfall zone; SRZ: summer rainfall zone; H: High pressure atmospheric circulation system; L: low pressure atmospheric circulation system; solid arrows: atmospheric currents; dashed arrows: oceanic currents; red stars indicate study site locations.

Namaqualand is located in the west of South Africa adjacent to the west coast and extending some 200-300 m east onto the Central Plateau of Southern Africa. While classified as a semi-arid winter-rainfall desert, the geography and topography of Namaqualand and surrounding ocean and atmospheric circulation systems cause a very spatially variable climate (Figures 3.2, 3.3). MAP ranges from only 50 mm at the arid coastal north to over 400 mm in the more mesic Kamiesberg mountains in the

east (Cowling, et al. 1999). Rainfall regimes, though variable spatially, have been described as predictable and reliable with low variability in seasonality (Hoffman and Cowling, 1987; Todd and Hoffman, 1999). The cold ocean has profound influence on regional climate. The Benguela Upwelling System causes very low sea-surface temperatures, reducing potential evaporation and rainfall delivery. The prevailing winds of the South Atlantic Anticyclone deliver this dry air from the west to Namaqualand causing arid summers. In winter, the anticyclone shifts northwards, as do the winter-rain bearing westerlies storm track (Figure 3.1) (Nicholson, 2000). In the north east, towards the edge of the nama karoo biome, summer convective precipitation events become an important contributor to annual rainfall (MacKellar, et al. 2007).

The southern Cape climatic system is, at present, influenced by a number of interacting factors (Figure 3.1). First seasonal expansion and northward propagation of the rain bearing westerly system delivers moisture during winter depressions. Second, tropical easterly flows that transport moisture associated with warm Indian Ocean water in summer. Third, multiple complex interactions emerge between these winter (temperate) and summer (sub-tropical) rainfall systems (Chase, et al. 2013; Tyson and Preston-Whyte, 2000). In short, these factors cause the southern Cape climate to be substantially more mesic than that of Namaqualand and the Kamiesberg. High potential evapotranspiration in summer under high temperatures is offset by ample moisture advection and delivery associated with the Agulhas Current, while in winter depressions associated with the westerlies deliver ample moisture. As a result, there is no pronounced dry season, making the southern Cape environments among the most mesic and biologically hospitable in southern Africa (Figure 3.2, 3.3).

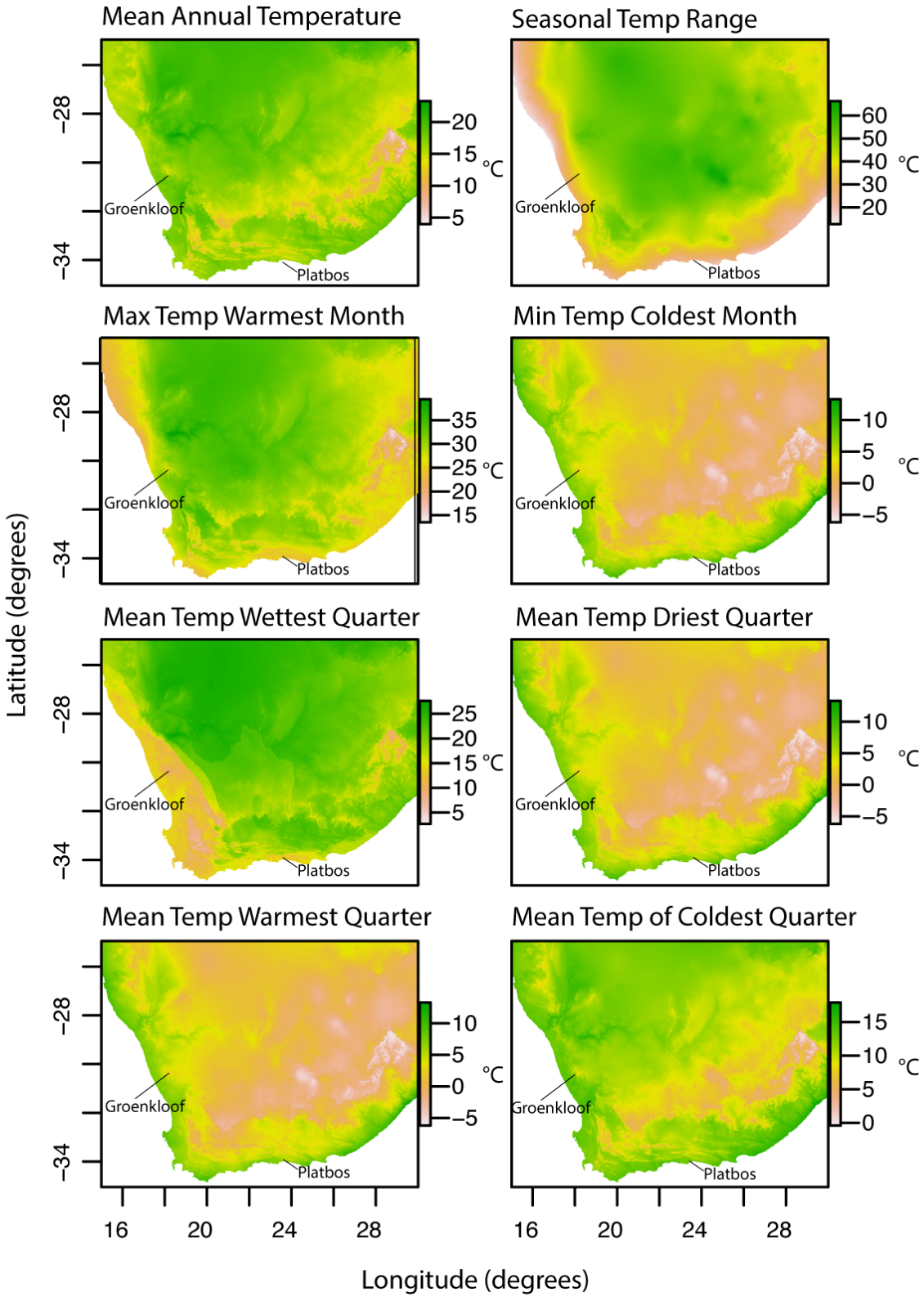

Figure 3.2. Biologically relevant temperature variables for southern Africa. Data from worldclim.org (Hijmans, et al. 2005).

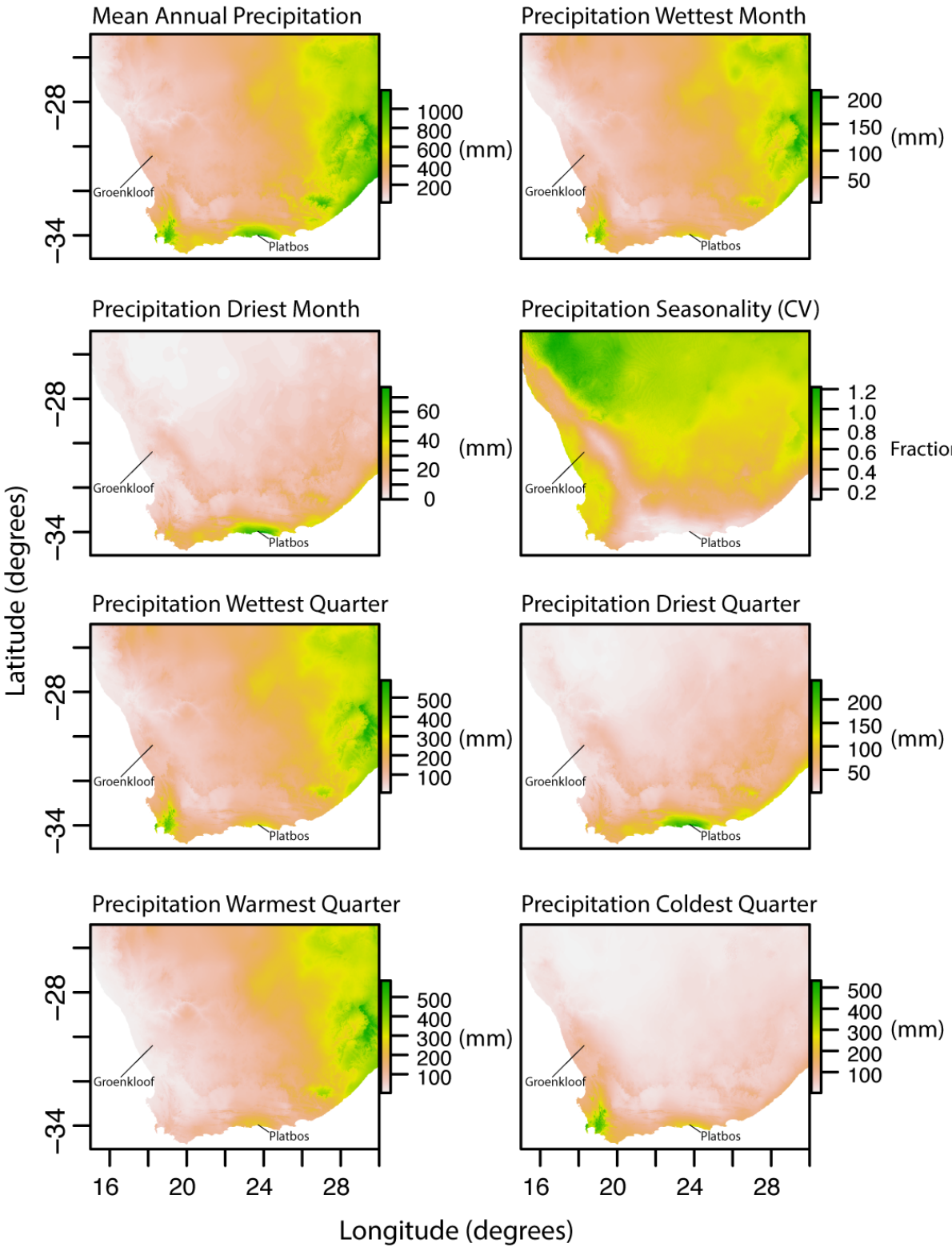

Figure 3.3. Biologically relevant precipitation variables for southern Africa. Data from worldclim.org (Hijmans, et al. 2005).

Though the geology of South Africa is complex, some broad generalities can be made that are of relevance to this study. The south west region that is typically associated with the fynbos biome is dominated by quartzitic sandstones of the Cape Supergroup (Figure 3.4). This is interspersed with less extensive shale patches of the Malmesbury, Kaaimans, Gamoots and Kango Groups, the Cape Granite Suite, as well as impermeable siltstones and mudstones of the Uitenhage Group. The region associated with succulent karoo and Namaqualand is dominated by Granites of the Namaqua and Natal Metamorphic Provinces. Further inland sedimentary deposits of the Dwyka and Ecca Groups dominate and are associated with the Karoo Basin and wider Karoo Supergroup (Council for Geoscience, 2016).

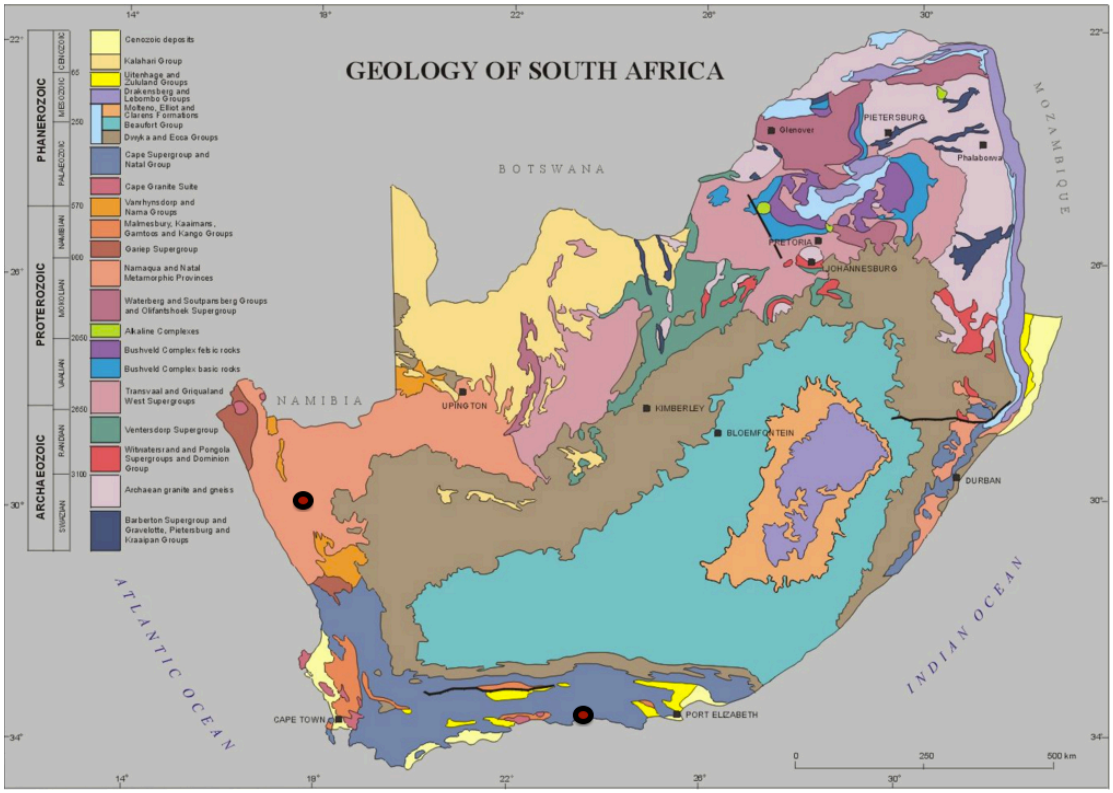

Figure 3.4. Generalised geological map of South Africa (Council for Geoscience, 2016). Red dots indicate sites in this study at Groenkloof (upper left marker) and Platbos (lower central marker).

3.4. GROENKLOOF SITE DESCRIPTION

Groenkloof is located in the Kamiesberg Mountains (900-1500 m above sea level) at the arid extension of the present-day fynbos biome. Precipitation for the region varies

between <100 and around 450 mm per annum, falling mostly in winter (CV = 33%) (Todd and Hoffman, 1999). The Kamiesberg escarpment is approximately 50 km in width, surrounded by the WRZ Namaqualand Hardveld Bioregion (MAP = 150 mm, CV = 38%) to the north, south, west and east (Figure 3.5). Some 40 km east of the site a rapid transition from dominant winter rains to late summer/ autumn rainfall occurs where the Kamiesberg ecozone transitions to Bushmanland (Desmet, 2007; Mucina, et al. 2006). Therefore the Kamiesberg is located at an important interface between WRZ, YRZ and SRZ. The sediment core was extracted from a perennial wetland at Groenkloof, located at S 30°21'17. 06, E 18°07'03. 15, adjacent to the road between Leliefontein and Paulshoek (Figure 3.6). The core is located within an enclosed basin that accommodates fynbos, renosterveld and succulent karoo vegetation types.

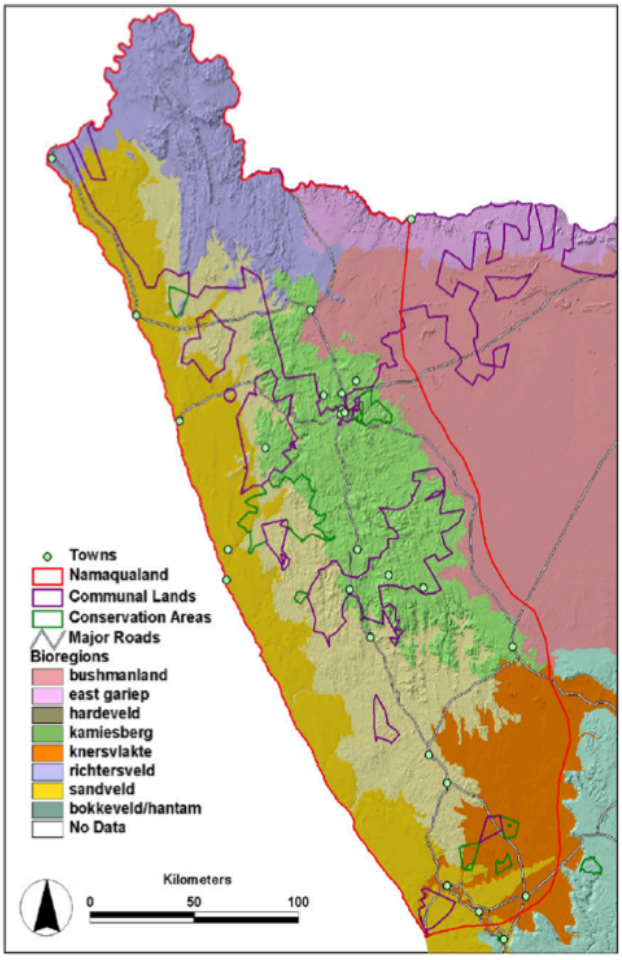

Figure 3.5. Regions of Namaqualand in the north-east of South Africa showing location for the Kamiesberg corner of South Africa (from Desmet, 2007).

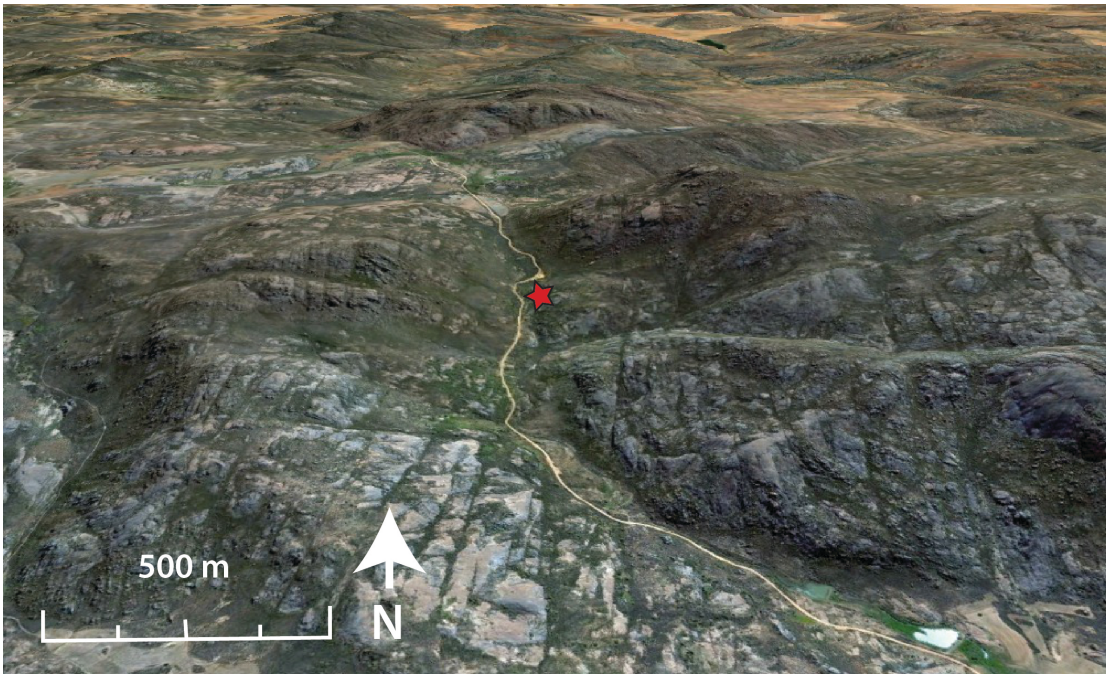

Figure 3.6. Location of the wetland in an enclosed basin at Groenkloof. The wetland and core location are indicated by the red star.

Kamiesberg Granite Fynbos occurs at the mid- to upper elevations of Groenkloof between around 1,530 m and 1,200 m a.s.l. in small pockets, or islands, within a matrix of renosterveld. It is tall, dense asteraceous fynbos (Rebelo, et al 2006). Localised patches occur on mountaintops within a renosterveld matrix, particularly at seeps and alluvial washes. Current prominent taxa include *Cliffortia ruscifolia, Metalasia densa, Anthospermum spathulatum* and *Ischyrolepis gaudichaudina*. It is also interspersed with thicket and succulent species (described below) in fire-free habitat such as rocky outcrops. Namaqualand Granite Renosterveld is distributed to the east of Kamieskroon and northeast of Garies in higher elevations of the Kamiesberg, extending to Paulshoek in the east, predominantly on mountain peaks and plateaus at altitudes 1,100-1,450 m a.s.l., where MAP is130-370 mm. It is a tall (1-1.5 m) shrubland with an understory of grasses, being particularly dominated by 'renosterbos' (*Elytropappus rhinocerotis*) and other asteraceous shrubs including *Chrysanthemoides monilifera*.

Kamiesberg Mountain Shrubland is a succulent and non-succulent dense shrubland, and is classified as part of the Succulent Karoo biome (Mucina and Rutherford, 2006). It occurs on steep or rocky south facing topography within Groenkloof. It is generally typical of more arid fynbos types with MAP around 230 mm, and occurs only at the lowest elevations within Groenkloof. It can be referred to as thicket-like with small trees such as *Rhus undulata* and *Dodonea visicosa.* More open areas are dominated by succulent and non-succulent shrubs such as *Aloe kamiesbergensis, Euphorbia mauritanica*, and *Eriocephalus* spp. Another succulent karoo vegetation type occurs slightly below Groenkloof on commercial grazing land that is referred to as Namaqualand Blomveld (Mucina, et al 2006) presumably due to the dominance of annual members of Asteraceae that produce renowned floral displays in spring. The altitudinal distribution of vegetation at Groenkloof is explored further in Appendix 1.

3.5. PLATBOS SITE DESCRIPTION

Platbos is located on the southern Cape coastal plateau to the northwest of Nature's Valley. Specifically, the site is presently a commercial pine plantation located on cleared former fynbos habitat north of the village of Covie, south of the Outeniqua Mountains and east of the Tsitsikamma Forest (Figure 3.7). Two perennial wetlands were located and cored at S 33.56.40.08 E 23.34.21.43 (Platbos 1) and S 33.56.30.01 E 23.34.36.18 (Platbos 2). Platbos 1 is around 160 x 20 m in size and situated around 800 m from the contemporary afrotemperate forest edge, while Platbos 2 is around 90 x 30 m and only 50 m away from the edge.

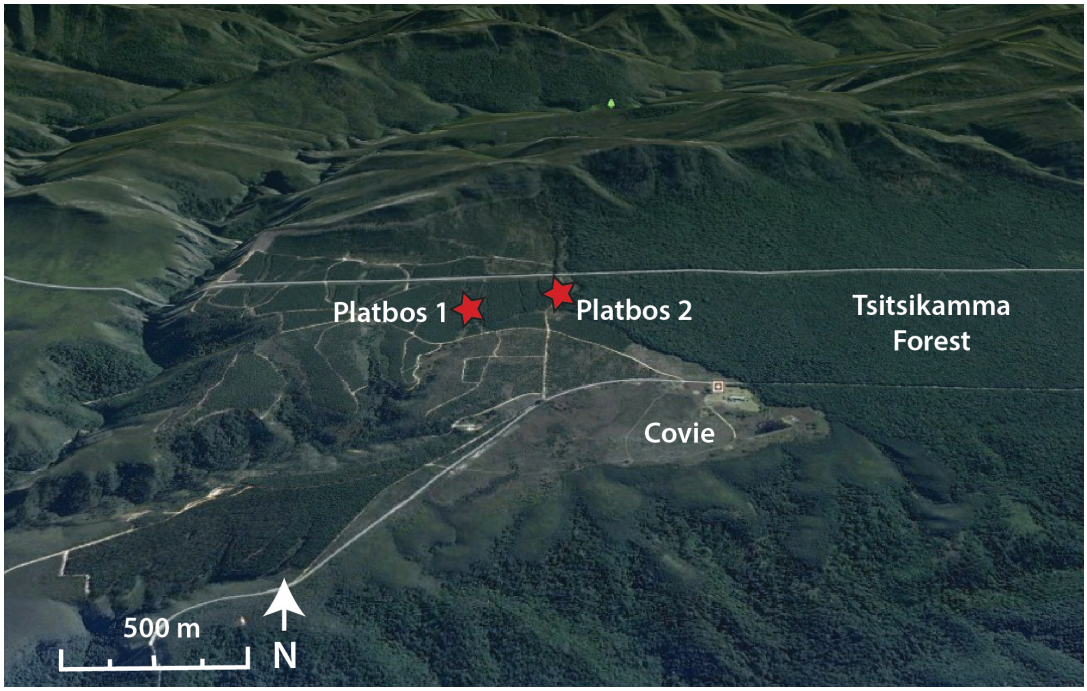

Figure 3.7. Location of Platbos 1 and 2. Note location on the plateau adjacent to Tsitsikama Forest.

These wetlands conform to what Vlok, et al (2008) identify as the Tsitsikama Pans. At present these often hard to identify as forest canopy, or in many cases dense stands of alien trees and intensive agriculture cover them (as is the case at Platbos). In the past they were likely exposed water bodies with a distinct flora and fauna. When filled they contain fresh black acidic water linked with the drainage systems of the Tsitsikamma Perennial Streams. This is the case at Platbos, as at both sites water appeared to be flowing through the wetlands, though very slowly. Where sunlight is ample distinctive aquatics including *Aponogeton junceus* and *Nymphaea nouchali* are present in the water, but are mostly dominated by range of shade tolerant sedges (e.g. *Carpha glomerata*, *Epischoenus adnatus*, *Isolepis diabolica*, *Juncus* spp. and *Schoenoxiphium lehmannii*).

Vlok, et al. (2008) provide a detailed description of the vegetation of the southern Cape. They identify a number of units in the vicinity of Platbos. The first major type is the Grassy Fynbos Forest-Thicket Mosaic. It likely represents areas that were once dominated by afromontane forest (in wetter areas) or thicket (in drier areas) in the geological past. Fire gradually would have transformed the vegetation by converting forests to grassy fynbos, which now dominates over relatively small patches of thicket

and forest present in fire-protected sites. The Tsitsikamma Thicket-Grassy Fynbos sub-type is found on the coastal forelands in the Tsitsikamma and is associated with moist conditions. Key indicator species (in order of relative abundance) include: *Stenotaphrum secundatum, Eragrostis curvula, Tristachya leucothrix, Helichrysum petiolare, Stoebe plumosa, Erica fuscescens, Erica gracilis, Erica hispidula, Erica unilateralis, Erica ostiaria, Leucadendron salignum, Leucospermum cuneiforme, Protea coronata, Bobartia macrocarpa, Bobartia macrospatha, Struthiola parviflora, Helichrysum cymosum, Helichrysum patulum, Euryops munitus, Morella serrata, Morella humilis, Wahlenbergia rivularis, Selago corymbosa, Rhus chirindensis, Rhus crenata, Rhus pyroides, Rhus lucida, Rhus laevigata, Virgilia divaricata,* and *Tephrosia grandiflora*.

Montane Mesic Proteoid Fynbos (Vlok, et al. 2008) is widespread at mid-altitude sites of the mountains of the southern Cape, and is a major vegetation component of the Outeniqua Mountains the abut Platbos to the north. It is typically characterised by well developed canopy of overstory proteoid shrubs, mostly of *Leucadendron* and *Protea.* Broader-leaved taxa such as *Laurophyllus capensis* may also be present. Certain units are dominated by tall closed canopies with ericoid shrubs such as *Berzelia intermedia*. Restionaceae are also abundant, but not very species-rich. In many units they consist largely only of tall species such as *Cannomois virgata* and *Rhodocoma gigantea*. After fire a number of short-lived herbs and shrubs belonging mostly to the Asteraceae and Fabaceae are particularly abundant. Vlok et al. (2008) also mote that Cyperaceae and Poaceae are also often abundant for the first few years following fire, but they do not persist for long, as are rapidly shaded-out by taller shrubs in moist habitat. The Covie Coastal Proteoid Fynbos is similar to the aforementioned proteoid fynbos; however it occurs closer to the coast and its habit tends to be stunted. This is due to the more harsh coastal climate which is windier, more saline, and it is therefore slightly less mesic. Typical indicator species include of the Covie Coastal Proteoid Fynbos include *Cliffortia stricta, Felicia echinata, Metalasia pungens, Metalasia muricata* and *Relhania calycina ssp. lanceolata*.

Forest in the area is best described by Mucina and Gendenhuys (2006) as Southern Afrotemperate Forest. This type is widely distributed as occurs in the western, eastern

and northern Cape Provinces, however it often only exists in very small patches. The largest complex of forest patches is found in the southern Cape along the narrow coastal strip (250 km long) Mossel Bay in the west and Humansdorp in the east (the Knysna-Tsitsikamma forest region), where it typically persists on sheltered seaward slopes of the coastal plateau. These are typically tall, multilayered forests dominated by a small number of species of Podocarpaceae (*Afrocarpus falcatus* and *Podocarpus latifolius*), *Ocotea bullata, Olea capensis* subsp. *macrocarpa,* as well as thicket-type species such as *Pterocelastrus tricuspidatus, Platylophus trifoliatus* and *Virgilia* spp.,. the latter typically being found on forest edges. In rocky habitats and deep-gorges *Cunonia capensis, Heeria argentea, Metrosideros angustifolia, Podocarpus elongatus* and *Rapanea melanophloeos* predominate. An understory of shrubs and herb layers are usually well developed, especially in more mesic habitats.

3.6. SEDIMENT EXTRACTION AND CLASSIFICATION

Sediment analysis yields valuable information relating to both palaeoenvironmental reconstruction and taphonomic processes that may have affected environmental and biological proxies. The core Groenkloof 3 was extracted from the centre of the sedimentary basin (Glew, et al. 2002). Extraction was undertaken using a vibracorer which works by generating high-frequency vibrations to fluidize sediments, enabling them to be drawn into aluminium tubing (Meadows and Baxter 2001). A bung was then placed into the top of the tubing in order to create a vacuum that allows the tubing to be extracted from the sedimentary deposits whilst retaining the enclosed sediment. Extraction was aided by use of a tri-pod winch. Following this, the tubing was halved length-ways using a circular saw. Prior to laboratory analysis the surface of the sediment material was scraped off using a razor blade to remove potentially contaminated material that may have been deposited during the extraction and splitting of the core. The same approach was used on two wetlands on the Platbos Plateau, hereafter Platbos 1 and Platbos 2, except for that it was not necessary to use a winch for extraction nor fluidise the sediments.

Sediments of all three cores were described and classified using widely used standardised schemes, namely the Troels-Smith classification scheme (Troels-Smith

1955) and the Munsell soil colour chart (Munsell Colour Company, 1954). Compositions of total organic carbon (TOC) and total inorganic carbon (measured as carbonate, TIC) within the core was then determined by loss-on-ignition (LOI). Sediment of volume 2 cm^3 was extracted incrementally through the profiles, weighed, dried in a drying cabinet, and weighed again. The samples were weighed, placed in porcelain crucibles and combusted in a muffle furnace at 500°C for 12 h to determine TOC content and for a further 12 h at 800°C for TIC. Numerous methods for LOI are used in palaeoecological analyses, but this combustion process is optimal for accurate measurements of wetland sediment according to Wang et al (2011).

3.7. CHRONOLOGIES AND AGE MODELLING

Radiocarbon dating is perhaps the most commonly applied dating technique in palaeoecological studies; particularly those of Holocene age (e.g. Roberts, 1997). It is therefore used as the primary dating technique here. ^{14}C atoms are produced in the upper atmosphere where cosmic ray neutrons displace a proton in ^{14}N to form the radioactive isotope ^{14}C ('radiocarbon'). Radiocarbon atoms interact with oxygen to form $^{14}CO_2$ and enter the biosphere through photosynthesis and assimilation of plant tissue by consumers. ^{14}C gradually decays to ^{14}N through beta decay, but is continually produced in the atmosphere and therefore replenished in plant and animal reservoirs. A state of isotopic equilibrium between carbon in the atmosphere and in plant and animal tissue is attained. Following death, assimilation of ^{14}C ceases as beta decay gradually reduces the amount of radiocarbon in plant or animal tissue. The half-life of radiocarbon is known (5,730 yrs), therefore time since death can be measured from the remains of plant materials (Björck and Wohlfarth, 2001).

The amount of ^{14}C in a sample can be measured using an accelerator mass spectrometer (AMS). AMS dating allows dating of relatively small amounts of material compared to 'traditional' beta decay approaches (Lowe and Walker 1997). This potentially allows higher precision in dating of the cores. Some caution is necessary in this interpretation due to the nature of the sediments being dated in this study. Continuous incorporation of organic matter into the sediment deposit means that measured radiocarbon ages are likely to be younger than the 'true' ages of the

sediment samples. Similarly, variations in the hydrological balance of the wetland can mobilise ^{14}C through the sediment column (Wang, et al. 1996). The humin of the sediment is less mobile than the humus, therefore this carbon fraction was isolated for AMS radiocarbon dating in all samples. Other problems associated with dating of wetland sediments include root penetration and bioturbation (Lowe and Walker, 1997). In order to avoid error associated with the former, roots can be avoided as much as possible during sample extraction.

Variations in atmospheric ^{14}C content are known to occur due to a multitude of factors, including cosmic ray fluxes caused by variation in Earth's geomagnetic field and changes in the intensity of solar activity, and changes in ocean circulation (Lowe and Walker 1997). This complicates the calculation of ages as variations in measured ^{14}C could reflect both decay (i.e. time since death) and the (variable) proportion of ^{14}C at the time of death. This problem is addressed by calibrating AMS ^{14}C results against reconstructed atmospheric ^{14}C concentrations such as those of Hogg, et al. (2014).

A chronology for Groenkloof 3 was established by means of accelerator mass spectrometer (AMS) radiocarbon dating. Three radiocarbon ages were determined by measurement of the bulk sediment. The humin fraction of the sediment was isolated and measured for its carbon isotope content to reduce methodological error associated with carbon mobility within the sediment column. Analyses were performed by Prof. P. Reimer at the school of Archaeology and Palaeoecology at Queens University Belfast. The radiocarbon ages were calibrated to calendar years using the SHCal04 radiocarbon calibration curve (McCormack et al. 2004) in the software BCal (Buck, et al 1999; http://bcal.sheffield.ac.uk). An age model was subsequently constructed using linear interpolation between each calibrated age with the surficial sample nominally representing -60/ 2010 AD, though it is acknowledged that the surficial sediments likely represent an amalgamation of multiple decades of pollen accumulation.

Four AMS radiocarbon dates in total were obtained for Platbos 1, again from the humin fraction of bulk sediment. The material was analysed at Queens University Belfast and also Beta Analytic Inc, Miami, Florida. Subsequent age modelling was

done in the package CLAM (Blaauw, 2010) for the open source software RStudio (2014) using the IntCal3 Southern Hemisphere calibration curve (Hogg, et al. 2014). In the upper portion of the cores, where radiocarbon dating is made problematic due to anthropogenic carbon emissions, exotic pollen markers were used in conjunction with historical records to infer approximate calendar dates. The first European settlement in the southern Cape was founded around 290 cal yrs BP/ c. AD 1660 at Plettenberg Bay, and planting of pine trees ensued promptly (Adamson, 1938). The point in the core at which pine pollen begins to occur was therefore assigned a date of 290 cal yrs BP/ c. AD 1660. A further more dramatic increase in pine pollen in the record is assumed to represent European settlement directly at Platbos which occurred later, between c. AD 1870 and 1880 (Phillips, 1926). This point in the pollen records was assigned a date of 75 ± 5 yrs cal BP/ c. AD 1875.

The calibrated radiocarbon ages and historical dates for Platbos 1 and 2 were then incorporated into comprehensive age models. The best-fit line passes through the midpoints of the highest probability density ranges, and stepwise point estimates were linearly interpolated for every 1 cm depth in the core (Blaauw, 2010). Weighted probabilities were calculated based on 1000 iterations per run of the model, and several runs were performed on each respective model to ensure consistent performance. The model goodness goodness-of-fit was consistently < -log 3, confirming adequate performance.

3.8. PALYNOMORPH EXTRACTION AND ANALYSIS

Pollen analysis been widely applied in understanding fynbos, particularly in elucidating past climate-vegetation interactions (Chase and Meadows 2007) and understanding of long-term fynbos resilience (e.g. Quick, et al. 2011; Valsecchi, et al. 2013). The identification of coprophilous fungal spores in pollen slides has recently furthered such applications in the region (Forbes, 2014). Analysis of fossil pollen and spores from the sediment cores was undertaken by extracting 1 cm^3 aliquots of sediment 0.5 cm in vertical width incrementally through the core. The most commonly adopted method for extracting palynomorphs pollen and spores from sediment cores was used and is described and reviewed in detail elsewhere (Bennett

and Willis 2001; Moore, Webb and Collinson 1991). Briefly, it involves the removal of unwanted sediment fractions by chemical digestion using strong acids and alkalis. NaOH is first used to remove humic acids. Hydrofluoric acid (HF) and hydrochloric acid (HCL) are used to remove silica and silicates (Assarsson and Granlund 1924), and acetolysis is employed to remove polysaccharides such as cellulose (Erdtman 1933).

Palynomorphs (pollen and spores) were identified using a Leica DM 750 high powered light microscope at x400 and x1000 magnification. Identification of pollen was facilitated by use of published sources including the African Pollen Database (2004), as well as the pollen reference collection in the Botany Department, University of Cape Town. New reference material was also created from herbarium specimens from the Bolus Herbarium, University of Cape Town, or from live specimens collected in the field. Pollen data are presented as proportions of the total land pollen sum (TLP). At least 250 land pollen grains were enumerated per sample (though this was lower for samples occurring after establishment of the pine plantation). This threshold value has been widely adopted in fossil pollen studies in the Cape to ensure an adequate representation of parent plants in the landscape (e.g. Sugden, 1993; Meadows and Baxter, 2001; Scott and Woodborne, 2007; Quick, et al. 2011). Spores of coprophilous Sordariaceae were identified with reference to Almeida-Lenero et al (2005) and Gelorini et al (2011), as well as personal correspondences with B. van Gael and A. Ekblom. This type is an aggregate of *Podospora*-type and *Sordaria*-type, which have been suggested among the most reliable indicators of large herbivore abundance (Baker, et al. 2013).

Extraction of macrocharcoal and microcharcoal can be incorporated easily into the standard pollen and spore extraction method (Bennett and Willis, 2001) Microcharcoal (<150 μm) was retained in the pollen and spore extraction and enumerated by use of the point-count method (Whitlock and Larsen 2002), which facilitates the calculation of the surface area of charcoal per unit volume of sediment expressed as cm^2 cm^3. Fragments were further divided into a size classes 3-12 μm, 13-25 μm, 25-50 μm and 50-150 μm in order to determine if attrition during the fossil extraction procedure distorted the charcoal data. At least 200 items (i.e. the sum of

charcoal fragments and Lycopodium) were counted per sample to ensure statistical significance (Finsinger and Tinner, 2005). Fossil macrocharcoal (>150 µm) was separated from the same sediment samples by sieving. Macrocharcoal was enumerated using a dissecting microscope as the total number of fragments per 1 cm^3 sediment.

3.9. DATA HANDLING

Palynological data was enumerated using the counting software CF Pollen Counting. Data are presented as percentages of the sum total pollen of terrestrial origin. Pollen concentrations were also calculated using the equation of Benninghoff 1962) to identify any artificial trends resulting from transforming the data to proportions, and the percentage dataset was deemed reliable for interpretation. A lower threshold for inclusion of pollen taxa in the pollen diagram was set at of ≥ 2 % of total land pollen (TLP) in any one sample in order to exclude pollen transported by wind or water in long distance dispersal events that might cause misinterpretation of local plant community dynamics (Sugita, 1994). Two unidentified pollen types ('PLB undiff 5' and 'PLB undiff 8') represented ≥ 2 % of the TLP but are excluded from the diagram and other analyses as taxonomic ambiguity renders them ecologically uninformative. Both taxa were relatively rare and not dynamic. Possible wetland taxa are excluded from the total pollen sum to reduce distortion of the fynbos/ forest pollen signal. These are expressed as accumulation rates rather than relative to the pollen sum to ensure that these environmental indicators are independent from the pollen spectra which for which they are used as explanatory variables. Fossil spore data are also presented independent of the total pollen sum as accumulation rates so as to avoid distortion of subtle trends by variability in the pollen data (Baker, et al. 2013).

Data were grouped into taxa definitive of fynbos, succulent karoo and afrotemperate forest to analyse between-biome relative abundance changes through time. This followed published biogeographic and floristic summaries of these biomes (Bergh, et al. 2014; Geldenhuys, 1991; Mucina and Rutherford, 2006) as well as the classifications used in fossil pollen studies elsewhere (e.g. Scott and Woodborne, 2007a, b; Quick, et al. 2015; Valsecchi, et al. 2013). Where it was not possible to

assign taxa to one biome, the grouping 'miscellaneous veld' (veld meaning vegetation) was used after Meadows and Baxter (2001). The pollen taxa Asteraceae long-spine and Poaceae are ubiquitous, have varied ecologies and can occur in significant abundance to both succulent karoo and fynbos. These taxa are therefore not assigned to a particular vegetation type in the study of that boundary. In contrast, based on the present distributions, composition and pollen taxonomy of fynbos and afrotemperate forest, Poaceae and Asteraceae long spine were reasonably assumed to represent fynbos taxa due to their scarcity within forest. Iridaceae could not be assigned to a particular biome at either study site.

Charcoal concentration data can be skewed by variations in sedimentation rate because of differing incorporation periods per unit sediment (Whitlock and Larsen, 2002). The macro- and microcharcoal concentration data were therefore converted to accumulation rates by expressing concentration as a function of age. A number of samples that contained extremely high charcoal contents which distorted trends in the data. A range of transformations were applied according to Juggins and Telford (2012) but did not adequately reduce distortion. Rather than arbitrarily exclude these outliers from the dataset, charcoal profiles both with and without these outliers were produced. These outliers are not considered erroneous hence this should not be considered a data 'cleaning' process – it simply serves to highlight more subtle changes in the charcoal record that would be masked by extremely high charcoal influxes or inappropriate data transformation.

Similarly, the most recent portions of the record are interrupted by clearance and/ or heavy modification of the natural vegetation at and around the biome boundary to varying degrees. The resulting trends in the pollen data were prominent and detracted from the key trends in biome dynamics resulting from changes in climate, fire and herbivory that were are the focus of this study. Although land-use change is a general focus of this study, the most recent changes associated with plantation forestry totally removed fynbos from the study site. This negated relevance of the change to the understanding of fynbos-afrotemperate forest dynamics. Samples associated with this plantation phase are therefore excluded from the analysis.

All palynomorph stratigraphic data were plotted using the palaeoecological software package C2 (Juggins, 2007). Each sample was assigned to an age in calendar years BP, as per the age models above, and the y-axis constrained by time.

3.10. STATISTICAL ANALYSIS

Quaternary pollen analysis is a quantitative discipline and typically uses statistical approaches to classify and describe complex multivariate stratigraphic data (Birks and Gordon 1985). Zonation techniques allows the delimitation of statistically significant portions of a pollen diagram stratigraphy (Legendre and Birks, 2012), and have been used to identify transitions between alternative stable states and other ecological transitions in pollen records (e.g. DeBoer, et al 2013; Gillson and Ekblom 2009; Gil-Romera, et al. 2010; Quick, et al. 2015). For Groenkloof 3 optimal splitting by least-squares was adopted as this technique that best described the major trends in the pollen sequence. This was performed in the software Psimpoll (Bennett, 2007). An additional sub-zone was identified qualitatively based on the abundance of the coprophilous fungal spores of Sordariaceae and corresponding subtle changes in the pollen spectra.

The number of statistically significant clusters in the Platbos 1 and 2 pollen diagrams were best identified using constrained hierarchical clustering in the packages ‘rioja’ (Juggins, 2014) and ‘vegan’ (Oksanen, et al. 2015) for R Studio (R Studio Team, 2015). A distance matrix incorporating all palynomorph taxa was first constructed using the Bray-Curtis method, and a clustering process was then performed on this matrix using the ‘CONISS’ method of agglomeration with clusters constrained by sample order (Birks and Gordon, 1985). The number of statistically significant clusters was determined by comparing the dispersion of the cluster analysis with that of random simulations in a scree plot using the broken-stick method (Oksanen, et al 2015).

Multivariate ordination methods serve a similar role to zonation in classifying and describing complex multivariate data, and can similarly be used to identify ecological transitions. However multivariate ordinations have two key advantages relevant to

this study. First, they further reduce noise that help to identify key ecological relationship between and among samples and taxa. Second, they are not stratigraphically constrained so can reveal ecological relationships between temporally distal taxa and samples (Legendre and Birks, 2012; McCune, et al. 2002).

Non-metric multidimensional scaling (NMDS) (Kruskal, 1964; McCune and Grace, 2002) has been suggested as the most robust method of unconstrained multivariate ordination in community ecology (Minchin 1987) and its utility in analysing fossil pollen data has recently been demonstrated (e.g. Broothaerts, et al. 2014, and references therein). NMDS has several advantages compared with other multivariate ordination techniques commonly applied to fossil pollen data, such as principal components analysis (PCA) and canonical correspondence analysis (CCA). It does not assume a linear response model (like PCA) or a unimodal response model (like CCA). Further, it does not require that the data be normally distributed, and therefore does not require transformation of non-normal data, and is particularly suited to the analysis of non-linear data. Further there are no 'hidden' dimensions as the number of dimensions is determined *a priori*, so less ecological information is lost (McCune, et al. 2002; Broothaerts, et al. 2014).

Non-metric multidimensional scaling (NMDS) was used to characterise the relationships between and among fossil pollen classes and samples. The analysis was performed in RStudio using the packages vegan (Oksanen, et al. 2015) and MASS (Ripley, et al 2014). First, a dissimilarity matrix of the data was generated using the Bray-Curtis method. The numbers of dimensions to be included in the ordinations were then determined by calculating 'stress'. This is an inverse measure of fit between rank orders of the original dissimilarity matrix and the NMDS ordination space data. Stress values of < 20 generally produce a usable ordination (Kruskal, 1964; McCune, et al. 2002). For all cores, at least a three dimensional solution was required to produce a stress value of between 10-15. Although addition of a fourth, fifth and sixth dimension improved (reduced) stress, they did not differ greatly from the second or third dimensions. The three dimensional solutions were therefore preferred. Where data values were larger than the common class scales, a Wisconsin double standardisation and square-root transformation were performed. Down weighting of rare (<5 % of TLP) taxa was performed to reduce distortion of the

model. Several model runs were performed to be confident that a global solution was found.

4. THE FYNBOS-SUCCULENT KAROO TRASITION AT GROENKLOOF

The resilience of fynbos at its semi-arid margins is likely to be tested over coming decades by changes in climate, fire and land use (Ackerly, 2014; Doblas-Morales, et al., 2015; Keeley, 2012). Its ecosystems have been identified as vulnerable to species range shifts, contractions and extinctions (Bomhard, et al. 2005; Driver, et al. 2012; Hannah, et al. 2005; Midgley, et al. 2002, 2003; Rutherford, 2000); biome shifts, including the replacement of fynbos with succulent karoo (Rebelo, et al. 2006; Wilson, et al. 2015); and regime shifts towards resilient alternative stable states dominated by invasive generalist species such as *Elytropappus rhinocerotis* (Slingsby, et al. 2014). Predictions of the threats posed to fynbos ecosystems and species are however hypothetical scenarios, and tend to overlook complex ecological processes and interactions (Altweg, et al. 2014). Palaeoecology offers a window into the long-term nature of ecosystem dynamics at the fynbos-succulent karoo transition that will allow empirical testing of hypotheses regarding the nature and causes of between- and within-biome dynamics (Quick, et al. 2011; Scott and Woodborne, 2007a, b; Valsecchi, et al. 2013), ecosystem state/ regime shifts (DeBoer, et al. 2013; Gillson and Ekblom, 2009; Gil-Romera, et al. 2010) and no-analogue and novel ecosystems (Jackson, 2006; also see Whittaker, 1975).

In ecosystems where resources are scarce, biota are often dominated by abiotic stress (Brown 1995; Darwin, 1859; Dobzhansky 1950; Louthan, et al. 2016; MacArthur 1972; Merriam, 1894; Schimper, 1903; Walter, 1971; von Humboldt, 1807). At the semi-desert margin of fynbos where aridity stress is high, it should be expected therefore that taxa respond fluidly to environmental change and closely track climate dynamics (Curtis, 1959; Jackson and Blois, 2015; Jackson and Williams, 2004; Whittaker, 1975). However biotic interactions and processes, such as competition for resources and disturbances including fire and herbivory, have also been suggested as deterministic in the organisation and extent of vegetation at the fynbos-succulent karoo interface (Esler, et al. 2015; Rebelo, et al. 2006). At the biome boundary therefore, system dynamics could be characterised both by fluid dynamics with weak

internal control, and strong internal feedback resulting in community cohesion (Connell and Ghedini, 2015; Collins, et al. 1992; Clements, 1936).

During cool, glacial phases of the Quaternary Period, equatorward propagation and intensification of the westerlies temperate storm track has resulted in enhanced winter rainfall in the GCFR (Chase and Meadows, 2007). This effected more mesic regional conditions than in the present interglacial, and fynbos expanded into regions currently occupied by dry succulent karoo. During interglacial phases, the winter rainfall system weakened and contracted, leading to aridification and recession of fynbos to cooler refugia at higher latitudes and altitudes (Chase and Meadows, 2007; DuPont, et al. 2007; DuPont, 2011). The flow of moisture from sub-tropical climate systems to mountainous regions of the Cape Fold Belt during summer has been suggested as key in determining fynbos persistence in the geological past by reducing summer aridity stress (Quick, et al. 2011; Valsecchi, et al. 2013). The resilience and longevity of fynbos evolutionary lineages is therefore likely dependent on the capacity of fynbos to retreat to such refugia (Bakker et al. 2005; Deacon, et al. 1992; Dynesius and Jansen, 2001; Jansen and Dynesius, 2000; Linder, et al. 2005, 1992; Verboom, et al. 2009) and subsequently recover its broader regional distribution when conditions ameliorate.

A fundamental limitation in understanding bioclimatic distributions in the past, present and future is that the present ranges for species and biomes may not reflect their potential distributions and climatic tolerances (Altweg, et al. 2014); but rather a realised niche defined other ecological parameters (Whittaker, 1975). Ecohydrological research on drought resistance in fynbos (Agenbag, et al. 2007; Mustart, et al. 2012; West, et al. 2012) suggests that some fynbos functional types may have a higher drought resistance capacity than expected, employing physiological adaptations such as stomatal regulation and rooting depth. However, responses to drought are highly variable within fynbos communities. Mature woody plants tend to be highly resistant to drought, while herbaceous and shallow rooted taxa are sensitive to summer desiccation (Altweg, 2014). Resistance to drought response should be expected to lead to fragmentation of the fynbos community, seasonality being a particularly strong environmental filter. Similarly, differing plant

functional responses to fire, such as between fire-stimulated and fire independent recruitment strategies (Ojeda, et al. 1998), may lead to fragmentation of the fynbos community along functional axes. Interactions among climate and fire are particularly important, pre- and post-fire conditions being sensitive to ecological processes owing to the high diversity of drought- and fire- adapted traits within the biome (Keeley, et al. 2012). The long-term resilience of some fynbos lineages and functional types may therefore be more dependant refugial populations than others, leading to internal shifts in community composition.

It is yet to be determined whether high fynbos resilience reflects continued recovery through climatic buffering of mesic mountain refugia, high physiological resistance to drought, or a combination of these two factors (Altweg, et al. 2014; Verboom, et al. 2009).

This chapter therefore explores the capacity for fynbos to resist change through physiological adaptation, as well as to mitigate climatic variability through persistence in refugial populations and subsequently recover. Over much of the fynbos biome the fynbos-succulent karoo transition is sharp, which reflects modification of the aridity gradient by soil texture. This sharp transition is further emphasised by the contrasting flammability and fire tolerances of the two biomes (Esler, et al 2015). In the Kamiesberg Mountains, Namaqualand, the fynbos-succulent karoo transition occurs in the absence of stark substrate contrasts and is more gradual. This will emphasise the effects of climate, fire and herbivory on biome dynamics.

4.1. GROENKLOOF 3 RESULTS

4.1.1. Sediment Description.

The core is 209 cm in length and four broad groupings emerge upon visual inspection (Figure 4.1, Table 4.1). The lowermost (GRNK3-A, 209-176 cm) is believed to represent the base of the deposit and consists of sand and gravel, but did not contain pollen. The overlying unit (GRNK3-B, 175-144 cm) consists mostly of highly humified peat and some sand. Stratigraphically above this is a highly variable unit

(GRNK3-C, 143-60 cm) with intercalated sand and peat components, but is primarily minerogenic. The uppermost unit (GRNK3-D, 59-0 cm) is composed of highly humified peat. No erosional contacts were observed between units.

Generally organic carbon (TOC) is of a much greater abundance than is total inorganic (TIC) carbon in the core (means = 15 and 0.8 %, respectively) (Figure 4.1). Both types exhibit similar trends through their respective profiles. Concentrations in sediment unit GRNK3-B (175-144 cm) are between 2-11 % (TOC) and 0.1-0.8 % (TIC) and peak to 15 % in unit GRNK3-C (143-60 cm). Values decrease particularly after around 120 cm (<2 % TOC; <0.1 % TIC). At around 95 cm depth an increase occurs to 12 % TOC and 1.0 %TIC. Carbon is then low (<5 % TOC; <0.4 %TIC) again until the onset of the uppermost unit GRNK3-D (59-0 cm), which contains the highest carbon proportions of 6-22 % TOC and 0.4-1.5 % TIC .

Table 4-1. . Groenkloof 3 sediment description.

Depth (cm)	Troels-Smith	Description	Munsel	Colour	Sediment unit
59-0	Ld44, Ga+	Highly humified peat with a trace of sand.	2.5YR, 2.5/1.	Black	GRNK3-D
143-60	Ld41, Gs1, Ga1, Gg+	Sands and gravels intercalated with highly humified peat.	10YR, 3/1.	Very dark grey	GRNK3-C
175-144	Ld43, Gs1.	Highly humified peat with some sand.	2.5YR, 2.5/1.	Black	GRNK3-B
209-176	Ga1, Gs1, Gg2	Sand and gravel, fining upwards.	7.5/YR, 5/1.	Gray	GRNK3-A

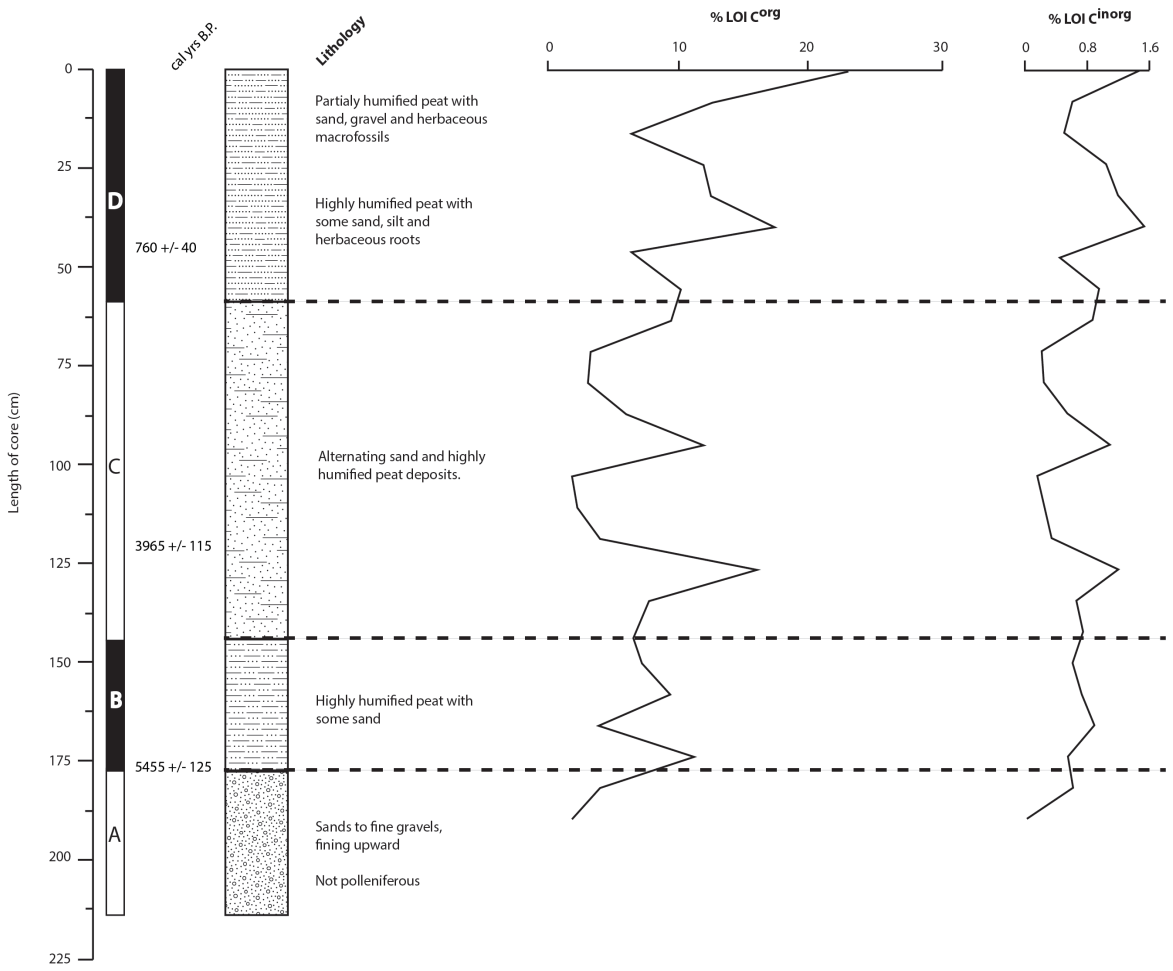

Figure 4.1.Groenkloof 3 sediment profile

4.1.2. Groenkloof 3 Chronology and Age Model.

Results of the AMS ^{14}C analysis are displayed in Table 4.3 and plotted in Figure 4.2. Mean median probability ages of, 5455 ± 125, 3965 ± 115 and 760 ± 40 cal yrs BP were obtained. These dates are amalgamated to construct the age-depth model for Groenkloof 3. Three phases of deposition with associated accumulation rates are identified in the age-depth model. Between ~5455 ± 125 and ~3965 ± 115 cal yrs BP material in the core accumulated at an average rate of ~0.4 mm/ yr-^{1}. From ~3965 ± 115 to ~760 ± 40 cal yrs BP the average rate is lower at ~0.2 mm/ yr^{-1}. The uppermost section, between ~760 ± 40 and -50 cal yrs BP, is modelled as accumulating at ~0.5 mm/ yr^{-1}. Within each of these successive phases therefore, each 0.5 mm depth sediment subsample extracted for fossil extraction and can tentatively be suggested to incorporate ~15, ~20 and ~10 years of average sediment accumulation, respectively.

Table 4-2. Groenkloof 3 radiocarbon dating results

Depth (cm)	Sample	Calibration data	Material type	^{14}C age	Calibrated age ranges (yrs BP)	Mean (95.4 %) cal BP age (AD where relevant)	Relative area under probability distribution
40-41	UBA-20281	IntCalSH13	Humified peat	898 ± 23	720-800	760 ± 40 (AD 1190)	1
120-121	UBA-20282	IntCalSH13	Humified peat	3690 ± 29	3850-4080	3965 ± 150	1
175-176	UBA-18621	IntCalSH13	Humified peat	4792 ± 34	5580-5330	5455 ± 125	1

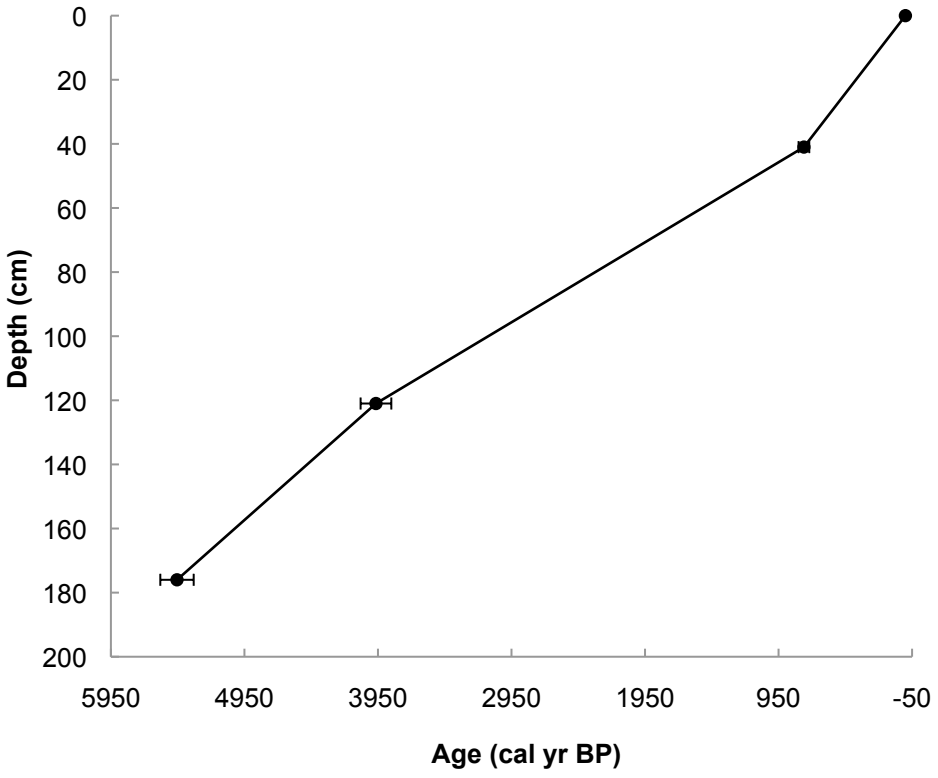

Figure 4.2. Groenkloof 3 age-depth model.

Optimal sequence splitting by least squares highlighted three significant assemblage zones in the land pollen data from Groenkloof 3 (Table 4.3). Based on visual analysis of the pollen spectra, as well as patterns in the abundance of coprophilous Sordariaceae fungal spores, an additional sub-division was added to the central zone.

Table 4-3. Details of Groenkloof 3 pollen diagram zonation.

`	**Depth ranges of constituent samples (cm).**	**Ranges of constituent samples (cal yrs BP).**	**Pollen zone boundaries (cal yrs BP).**
GRNK3-3	0-36	-50 to ~670	~705 to near present.
GRNK3-2b	40-67	~740 to ~1800	~1960 to ~705
GRNK3-2a	75-120	~2120 to ~3925	~3985 to ~1960
GRNK3-1	124-197	~4045 to ~5535	~5535 to ~3985

4.1.4. Groenkloof 3 Biome Aggregate Data

Aggregations of the pollen data based on putative biome affinity (see Chapter 3.4) shows that taxa of the groupings fynbos, succulent karoo and 'miscellaneous taxa' have persisted at Groenkloof for the entire extension of the record (Figure 4.3). There are however significant changes in the proportion of fynbos pollen in the Groenkloof 3 sequence. Fynbos is the dominant component of the pollen spectra through the record but is variable, constituting ~70-90 % of the total land pollen sum in GRNK3-1 (~5535 to ~3985 cal yr BP), ~55-85 % in GRNK3-2a (~3985 to 1960 cal yrs BP), ~55-80 % in GRNK3-2b (~1960-705 cal yr BP), and ~75-95 % in GRNK3-3 (~705 cal yr BP to near present). The minimum fynbos proportional abundance of ~55 % is cantered around 2000 cal yrs BP.

The succulent karoo grouping, in contrast to fynbos, is relatively rare and stable, varying between ~2 and ~10 % through the entire sequence. Higher proportional abundance generally occurs in the central zones (GRNK3-2a and GRNK3-2b), with a maximum of ~10 % being reached around ~2000 cal yrs BP.

The miscellaneous group of taxa, similarly to succulent karoo, is also most abundant in the central zones, but is markedly more abundant and dynamic. In the basal zone GRNK3-1, abundance varies between ~10-20 %. This then increases rapidly at the onset of zone GRNK3-2a, then increases variably to a maximum relative abundance of ~35 % by around ~2000 cal yrs BP. A steady decrease then occurs towards the top of GRNK3-1, where after in the uppermost zone, GRNK3-3, the proportion of miscellaneous taxa is ~10-15 %.

The lowermost and uppermost zones (GRNK3-1 and GRNK3-3 at ~5535 to ~3985 cal yr BP and ~705 cal yr BP to near present) seem at least partially analogous when taxa are aggregated according to biome associations. While the proportions in all zones are characterised by the pattern fynbos > miscellaneous > succulent karoo, this pattern is strikingly less pronounced in the central zones (GRNK3-2a and GRNK3-2b, ~3985 to 1960 and ~1960-705 cal yr BP), where fynbos pollen is reduced to approximately half of the pollen proportion. In zone GRNK3-2a the fynbos proportion is generally decreasing, while in GRNK3-2b shows a gradual increasing trend. In contrast, the lowermost and uppermost zones are have similar proportions of the aggregates (although miscellaneous and succulent karoo are slightly more prevalent in the lowermost zone).

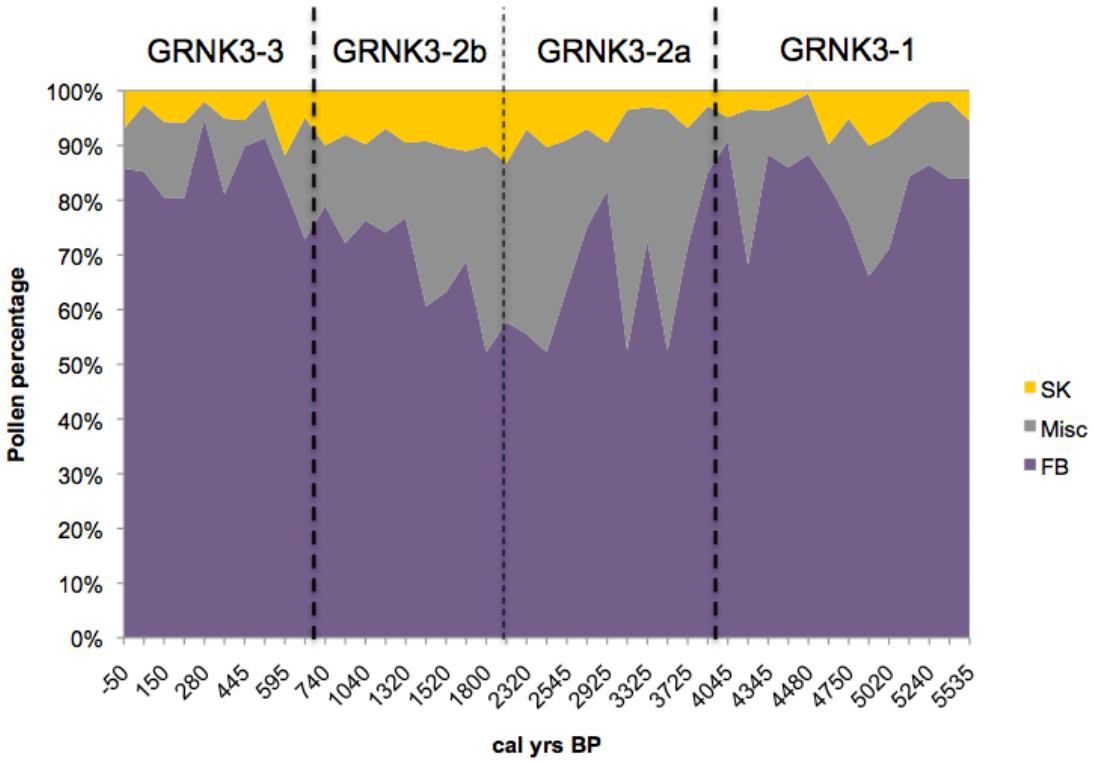

Figure 4.3. Groenkloof 3 biome aggregate data. SK = succulent karoo, Misc = miscellaneous, FB = fynbos.

4.1.5. Groenkloof 3 Pollen Diagram

The pollen diagram displaying identified taxa constituting ≥ 2 % of the pollen sum (see Chapter 3.9) for the Groenkloof 3 is given in Figure 4.4. (All pollen data is provided in Appendix 2). In zone GRNK3-1 (~5535 to ~3985 cal yr BP) the most prominent taxon is *Muraltia*, which fluctuates at high amplitudes between ~56 and ~3 % of TLP. High values of ~17-43, ~29 , ~56 and ~17-22 % are recorded around ~5535 to ~5020, ~4590, ~4345 and ~4210 to ~4045 cal yrs BP, respectively. Lower abundances of ~4 and ~3 % occur around ~4885 to ~4750 and ~4480 cal yrs BP. Abundances of the next most prominent taxon in this zone, *Cliffortia*, appear to loosely reflect an inversion of this pattern. Lower values of ~3-13 and ~11 % occur around ~5535 to ~5020 and ~4345 cal yrs BP. Higher abundances of ~36, ~48, and ~45 % are recorded at ~4750, ~4480 and ~4045 cal yrs BP, respectively. Restionaceae is most abundant lower in this zone, then declines variably through the sequence from ~21 % at ~5345 cal yrs BP to <5 % in the upper few samples. A notable peak to ~10 % is centred around ~4480 cal yrs BP interrupts this trend. Stoebe-type pollen generally declines through the zone from ~12 % at ~5535 cal yrs BP to ~5 % at ~4045 cal yrs BP, interrupted by peaks at ~5240 and ~4885 cal yrs BP. A similar pattern is exhibited by *Anthospermum*, which declines from ~23 to ~13 % between ~5535 and ~4045 cal yrs BP, interrupted by an increase at ~4885 cal yrs BP. Other fynbos taxa in this zone include Fabaceae, Malvaceae and *Clutia*-type, but these are rare (<3 %).

Of the miscellaneous group, Asteraceae long spine and Poaceae contribute significantly to the pollen sum. Asteraceae fluctuates between ~3 and 13 %,with no directional trend. Higher abundances are recorded between ~5020 and ~4750 cal yrs BP. Similarly, Poaceae fluctuates between abundances of ~0.5 and 16 %, with relatively high values from ~5020 to ~4750 and at ~4210 cal yrs BP.

Succulent karoo pollen types are not well represented in zone GRNK3-1. Aizoaceae, Crassulaceae, *Pentzia*-type, Chenopodiaceae, Geraneaceae and Asphodelaceae are all recorded, though in abundances of <5 %. The highest abundances within this group

are ~3.5 and ~4.5 % recorded for Aizoaceae and Crassulaceae, respectively, at ~4590 cal yrs BP.

The next zone is GRNK3-2a, which spans from ~3985 to 1960 cal yrs BP. Significant shifts in the abundance of fynbos taxa occur here. *Muraltia* pollen, while often very abundant in the previous zone, is not common in high abundances. Values range between ~14 and <1 %, with higher abundances at the base of the zone and between ~2925 and ~2645 cal yrs BP, and much lower elsewhere. *Cliffortia* is perhaps more consistently abundant than in the preceding zone. It declines variably in abundance upwards, from ~41 % at ~3925 cal yrs BP to ~11 % at ~2120 cal yrs BP. This declining trend is interrupted by an increase in *Cliffortia* abundance between ~2925 and ~2645 cal yrs BP. Restionaceae increases from by ~9 % compared to background levels at the start of the zone, then gradually decreases upwards reaching to ~3 % at ~2120 cal yrs BP. *Stoebe*-type is slightly more abundant than in the preceding zone, and its abundance generally fluctuates between ~8-15 %. Similarly, *Anthospermum* becomes slightly more abundant, typically being around ~15-20 %. Some of the less common taxa also show changes. Malvaceae occurs in significant proportions, with peaks of ~6 and 5 % at ~3325 and ~2120 cal yrs BP, and *Clutia*-type reaches >3 % at ~3325 cal yrs BP.

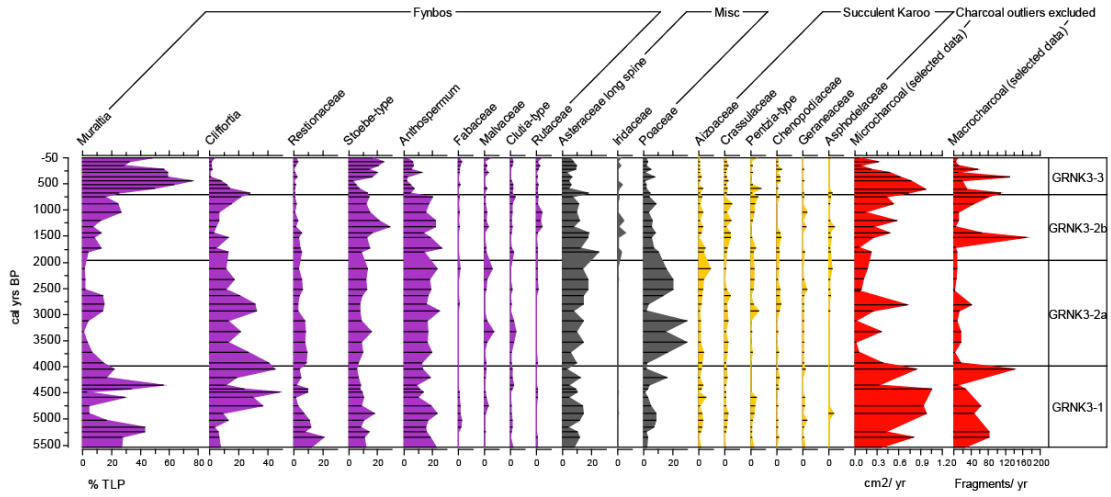

Figure 4.4. Groenkloof 3 percentage pollen diagram (includes all taxa constituting >2 % abundance relative to total land pollen). Charcoal data (with outliers removed – see Chapter 3.4) are also displayed.

The miscellaneous taxa in GRNK3-2a show appreciable trends, being a prominent feature of the pollen spectra. Asteraceae increases through GRNK3-2a from ~10 % at ~3925 to ~17 % at the top of the zone. Poaceae is much more abundant than in the preceding zone and is the dominant graminoid. Abundances range from ~13 to ~30 % through most of this zone, except for at ~3925, ~2925 and ~2805 cal yrs BP where values of <4 % are recorded.

Again, in GRNK3-2a, the succulent karoo taxa are not very abundant relative to those of fynbos nor the miscellaneous taxa. They are however slightly more abundant than in GRNK3-1, particularly towards the top of the zone. The most notable feature is a peak in Aizoaceae abundance to ~8 % at 2120, which is the uppermost sample in GRNK3-2a.

In the second portion of the central zone (GRNK3-2b, ~1960-705 cal yr BP) *Muraltia* pollen becomes abundant again, increasing from ~4 % at ~1800 cal yrs BP to ~27 % at ~1040 cal yrs BP, then declining to ~15 % in the uppermost sample at ~740 cal yrs BP. *Cliffortia* fluctuates between ~3 and ~13 % until the upper portion of the zone, whereupon it increases in abundance from ~6 % at ~1040 cal yrs BP to ~21 % at ~740 cal yrs BP. Restionaceae almost disappears from the record, accounting for <1 % of TLP by the top of this zone. *Stoebe*-type and Anthospermum exhibit little change in their nature and abundance compared with the preceding zone, except for a peak in the abundance of the former to ~28 % centred on ~1320 cal yrs BP. All other fynbos elements constitute <4 % each to the total pollen sum. Both Asteraceae and Poaceae decline through GRNK3-2b. The former from 25-7 % between ~1800 and ~740 cal yrs BP, and the latter from ~10-4 % over the same time period. In contrast to the dynamism expressed by the fynbos and miscellaneous taxa, the succulent karoo pollen types again show little change, with all abundances remaining below 5 %.

Perhaps the most prominent change in the whole Groenkloof 3 record occurs in the uppermost zone GRNK3-3 (~705 cal yrs BP- near present). *Muraltia* increases rapidly at the onset, from ~25 % at ~665 cal yrs BP to a peak of ~76 % at ~445 cal yrs BP. A sharp decline subsequently occurs, and abundances of 58-56 % then persist between ~370 and ~220 cal yrs BP. Another sharp decline to 29 % to at ~150 cal yrs

BP is followed by a resurgence to ~48 % in the sample at the surface of the core. *Cliffortia* is abundant at the onset of this zone (~27 %) then declines sharply to 0 % by 280 cal yrs BP. In the surface sample, only ~3 % is of *Cliffortia*. Both *Stoebe*-type and *Anthospermum* also record sharp declines from the onset of the zone. *Stoebe*-type reaches a low of ~5 % by ~445 cal yrs BP, then increases to 17 % by the top of the core. *Anthospermum*, similarly, reaches a low of ~2 % between ~445 and ~370 cal yrs BP, then subsequently increases to ~5% by the surface. Restionaceae, Fabaceae, Malvaceae, *Clutia*-type and Rutaceae are all rare, none constituting more than 3 % of the land pollen sum. Asteraceae and Poaceae are less abundant still, the former declining from ~18 % at ~665 cal yrs BP to ~5 % at the surface and the latter varying between ~7 and <1 %. As through much of the preceding record, succulent karoo taxa are rare (<3 %), with the exception of a peak in *Pentzia*-type pollen to 7 % at ~595 cal yrs BP.

4.1.6. Groenkloof 3 Fossil Charcoal.

A scatter plot of microcharcoal versus macrocharcoal (Figure 4.5) reveals a number of outliers, all of which are part of the lowermost zone GRNK3-1. At ~5160, ~5020 and 4210 cal yrs BP microcharcoal is markedly more abundant than in other samples, but macrocharcoal influx is not markedly different from the majority of other samples. At ~4590 cal yrs BP the inverse is true, macrocharcoal being high and microcharcoal low. Removal of these samples from the charcoal profiles reveals remarkably different trends, as influx of both charcoal size classes appears to be of similar magnitudes in zones GRNK3-1, GRNK3-2b and GRNK3-3, while in GRNK3-2a there is less charcoal.

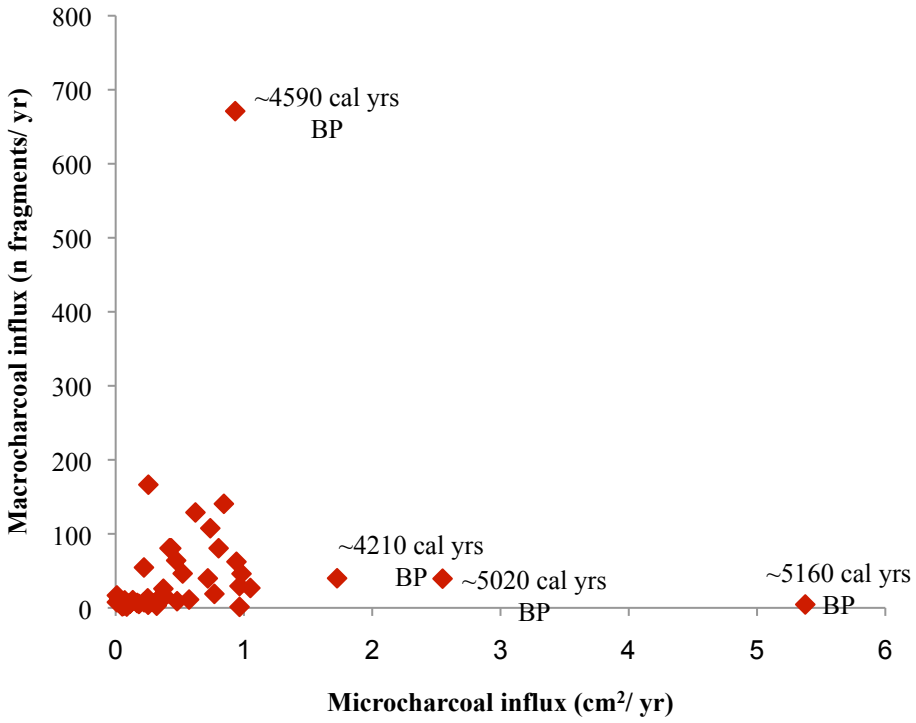

Figure 4.5. Groenkloof 3 charcoal influx scatter plot. Microcharcoal are plotted against macrocharcoal, expressed as influx rates (cm^2/ yr and n fragments/ yr, respectively).

The fossil charcoal data from Groenkloof 3 is displayed in Figure 4.6. The lowermost zone (GRNK3-1, ~5535 to ~3985 cal yr BP) contains the highest charcoal influx rates of any in the Groenkloof record for both macro- and microcharcoal. Macrocharcoal influx is highly variable, rates varying between <5 and ~670 fragments/ yr^{-1}. Significant amounts (> ~20 fragments/ yr^{-1}) are recorded in all samples with the exception of at ~5155, ~4480, ~4345 cal yrs BP, where influx is very low (< ~20 fragments/ yr^{-1}). A large spike in influx of macrocharcoal is recorded at ~4590 cal yrs BP, where the rate reaches ~670 fragments/ yr^{-1}. Microcharcoal influx rates are similar, though with some appreciable contrasts. Typically it is >0.8 cm^2/ yr^{-1}, and peaks of ~0.8, ~2.5, ~5.4 and ~1.7 cm^2/ yr^{-1} occur at ~5345, ~5020, ~4480 and ~4209 cal yrs BP. Much lower rates of influx (< ~0.5 cm2/ yr^{-1}) are recorded at ~5535, ~5155 and ~4345 cal yrs BP.

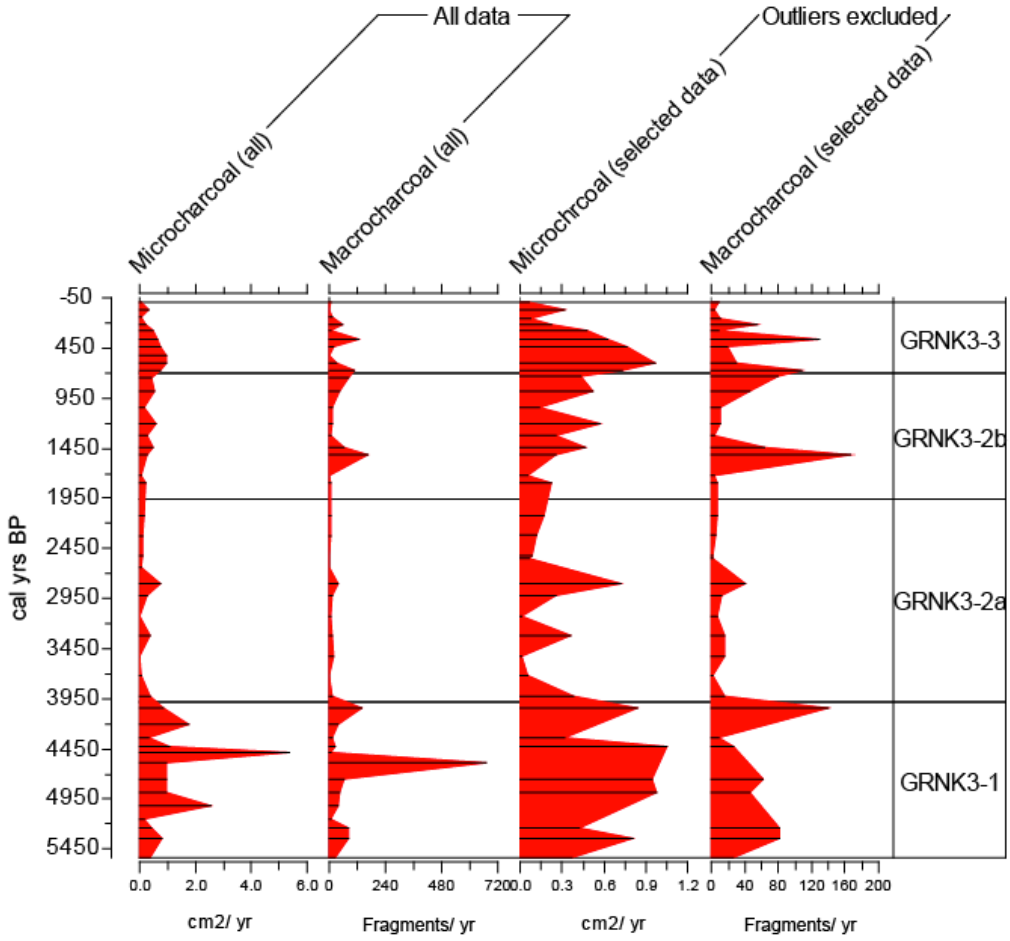

Figure 4.6. Groenkloof 3 fossil charcoal stratigraphic profiles. . Microcharcoal and macrocharcoal are expressed as influx rates (cm^2/ yr and n fragments/ yr, respectively). Profiles are presented including all samples (left) and with 'outlier' samples excluded (right) (see Figure 4.5).

In the following zone, GRNK3-2a (~3985-1960 cal yr BP) influx rates of both size classes are lower in than in the preceding zone. They are also the lowest of any zone in the Groenkloof 3 record. Macrocharcoal influx drops immediately at the zone onset to ~15 fragments / yr^{-1} at ~3925 cal yrs BP. Following this, the rate does not increase above ~17 fragments/ yr^{-1}, except for a slight peak to ~40 fragments/ yr^{-1} at ~2805 cal yrs BP. The trends in microcharcoal influx are similar. Slight peaks occur at ~3325 and 2805, but generally rates are very low at < ~0.25 cm^2/ yr^{-1}. Macrocharcoal influx in zone GRNK3-2b (~1960-705 cal yrs BP) is higher than in the preceding sub-zone GRNK3-2a, with highs of ~80 and ~115 fragments/ yr^{-1} centred around ~1520 and ~740 cal yrs BP. Microcharcoal generally increases upward through the zone, from ~0.22 at ~1800 to ~0.43 at ~740 cm2/ yr^{-1}.

The influx of macrocharcoal in GRNK3-3, the most recent portion of the record, is similar to in the preceding zone, with spikes at ~108, ~130 and ~55 cm^2/ yr^{-1} at ~665, ~370 and ~220 cal yrs BP, respectively. Microcharcoal influx is slightly higher than in the previous zone, increasing from ~0.73 to ~0.97 cm^2/ yr^{-1} between ~665 and ~520 cal yrs BP, and subsequently declining to < 0.07 cm2/ yr^{-1} by the surface of the core.

4.1.7. Groenkloof 3 Non-land Pollen and Non-pollen Palynomorphs

Pollen taxa that could be derived from either land or non-land plants, as well as spores/ non-pollen palynomorphs, are displayed in Figure 4.7. Only two non-land pollen taxa were identified in significant amounts. *Gunnera* influx in GRNK3-1 (~5535 to ~3985 cal yr BP) is typically between ~0 and ~600 grains/ yr^{-1}. Cyperaceae becomes increasingly abundant through the zone, peaking from around ~600 grains/ yr^{-1} at the base to ~1900 grains/ yr^{-1} by ~4210 cal yrs BP. In Zone GRNK3-2a (~3985-1960 cal yr BP) the influx rate of *Gunnera* is lower still, being between 0 and ~200 grains/ yr^{-1}. Cyperaceae influx is also lower than in the preceding zone, not reaching abundances of > ~800 grains/ yr^{-1}. Later, in Zone GRNK3-2a (~3985-1960 cal yr BP), *Gunnera* remains scarce with influx not exceeding ~250 grains/ yr^{-1}. The rate of Cyperaceae influx increases from < 500 grains/ yr^{-1} at the base of zone to ~1500 grains/ yr-1 by ~880 cal yrs BP, which is similar to the maximum reached in the basal zone. The uppermost zone, GRNK3-3 (~705 cal yrs BP - near present), is characterized by much higher values of both *Gunnera* and Cyperaceae than recorded in the preceding zones. Influx rates of ~1800 and ~3400 grains/ yr-1 are recorded for the respective taxa at ~370 cal yrs BP. Sharp declines to ~200 and ~300 grains/ yr^{-1} are recorded at ~280 cal yrs BP, and influxes then resurge to ~1800 and ~3900 grains/ yr^{-1} by the surface of the core.

Spores of *Zygnema*-type, *Riccia*-type, Sordariaceae and the morphological taxa monolete spores and trilete spores are displayed in Figure 5.7. Influx rates of all taxa are erratic, yet some trends are discernable.

In zone GRNK3-1 (~5535 to ~3985 cal yr BP) *Zygnema*-type is only of significant abundance in the lower most sample, where it accumulated at a rate of ~720 spores/ yr^{-1}. Influx peaks of *Riccia*-type of ~80 to ~160 spores/ yr^{-1} around ~5535, ~5020 and ~4045 cal yrs BP. Monolete spores are also only abundant in the most basal sample. Trilete spore influx rates are the highest of all the spore taxa. The taxon is present throughout the zone, with peaks to ~1200 and ~600 spores/ yr^{-1} occurring at ~4750 and ~4045 cal yrs BP, respectively.

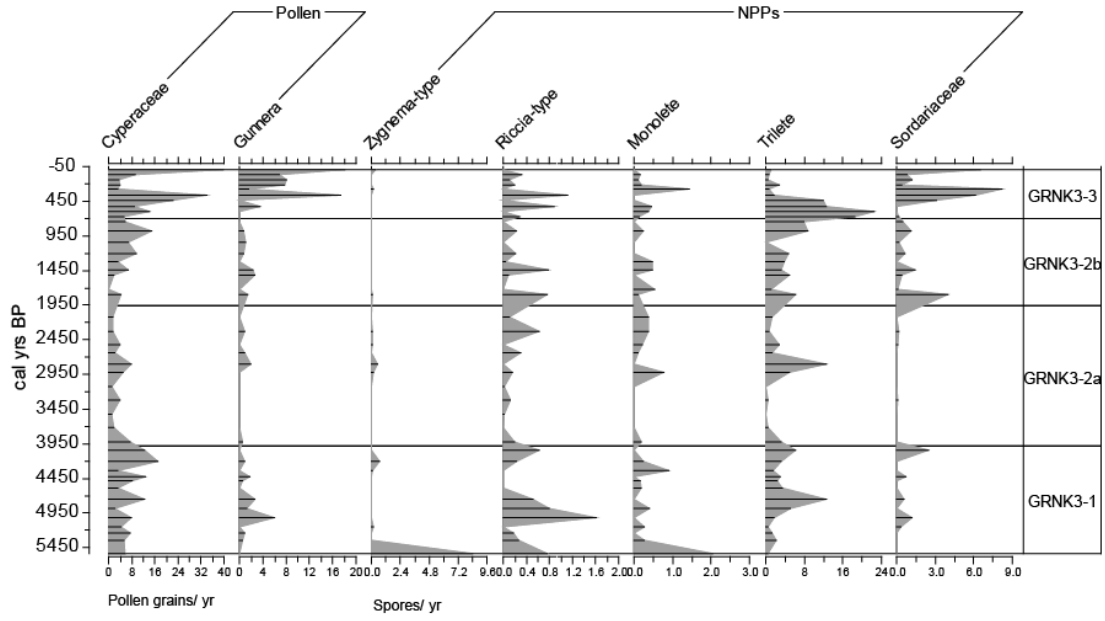

Figure 4.7. Non-land pollen and non-pollen palynomorphs from Groenkloof 3. Data are influx rates and are expressed as n spores/ yr x 10^{-2}

All spore taxa decline in abundance at the onset of zone GRNK3-2a (~3985-1960 cal yr BP). Most are absent or present at very low rates of influx (< 100 spores/ yr^{-1}) from the base of the zone until ~3125 cal yrs BP, whereupon *Riccia*-type, monolete spores and trilete spores increase in abundance and remain significant features of the record through to the surface of the core. Notable peaks in influx of *Riccia*-type occur ~2320, ~1800, ~1440, ~520 and ~370 cal yrs BP. Monolete spores peak at ~3325, ~1720, ~1800, ~670 and ~280 cal yrs BP. Trilete spores are again Trilete spores again are the most abundant spore type. Peaks occur at ~2805, ~1800, ~1440, and ~1320 cal yrs BP. Following this, between ~880 and ~520 cal yrs BP and peaking at ~6595 cal

yrs BP, trilete spores become very abundant with influx rates of between ~800 and ~2000 spores/ yr^{-1}. This latter trend is the most prominent feature of the spore record.

Following the reduction in all spore types at the onset of zone GRNK3-2a Sordariaceae does not increase in abundance until the onset of zone GRNK-2b (~1960-705 cal yr BP). A peak influx to ~350 spores/ yr^{-1} occurs at ~1800 cal yrs BP, thereafter rates are similar to in the basal zone. Between ~445 and ~150 cal yrs BP a striking increase in the influx rate occurs, peaking to ~820 spores/ yr^{-1} at ~280 cal yrs BP. The uppermost sample (~ near present) is also rich in Sordariaceae with an influx of ~650 spores/ yr^{-1}.

4.1.8. Groenkloof 3 Non-metric Multidimensional Scaling

A three dimensional solution produced an MNDS model with a stress value of ~18 (Figure 4.8). A plot of NMDS1 verses NMDS2 (Figure 4.8) shows that neither samples nor taxa are strongly partitioned through time and by biome/ aggregate taxonomic grouping. The only clear distinction is the segregation of samples from 595 to 0 cal yrs BP, primarily in association with *Muraltia*, Rutaceae, Fabaceae and Iridaceae. Almost no partitioning of samples and taxa through time is evident when NMDS1 is plotted verses NMDS3.

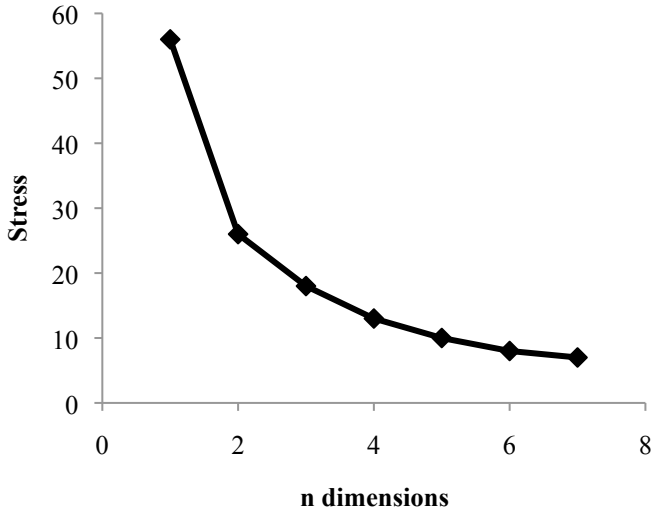

Figure 4.8. Stress plot for Groenkloof 3 NMDS model.

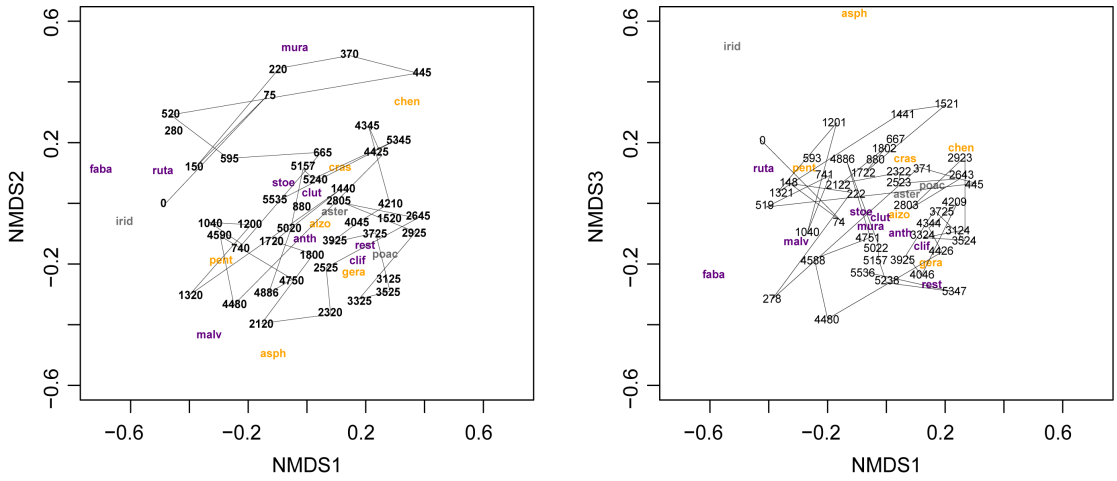

Figure 4.9. Groenkloof 3 NMDS bi-plots of dimensions 1 and 2 (left) and 1 and 3 (right).

4.2. PALAEOEENVRIONTS AND PALAEOECOLOGY OF GORENKLOOF 3

4.2.1. Zone GRNK3-1 to GRNK3-2a (5535-2130 cal yrs BP): Palaeoenvironmental Context

The basal zone of Groenkloof record (5,500-4,000 cal yrs BP) overlaps with the mid Holocene Altithermal (MHA, 8,000-4,000 cal yrs BP) which is characterised by the warmest (pre-industrial) Holocene temperatures across southern Africa (Chase and Meadows, 2007). Inferred palaeotemperatures vary across the sub-continent by between 1-3^{o}C warmer than present averages (Stute and Talma, 1998). Termination of the MHA is marked by regional cooling at 4,000 cal yrs BP termed the 'neoglacial' (Talma and Vogel, 1992). From 4,000 to 2,100 cal yrs BP a cooling is evident at both the Stampriet aquifer in east central Namibia (Stute and Talma, 1997) and at Uitenhage in the Eastern Cape of South Africa (Heaton, et al. 1983). Temperature decreases of magnitudes 0.5^{o}C and 3^{o}C are estimated, respectively. These estimates are broadly contemporaneous with cooler temperatures registered in the Cango Cave speleothem record from the southern Cape (Talma and Vogel, 1992), and the Tortoise Cave in the south western Cape (Jerardino, 1993). The transition between zones GRNK3-1 and GRNK3-2a therefore reflects a regional temperature gradient (albeit a cooling gradient).

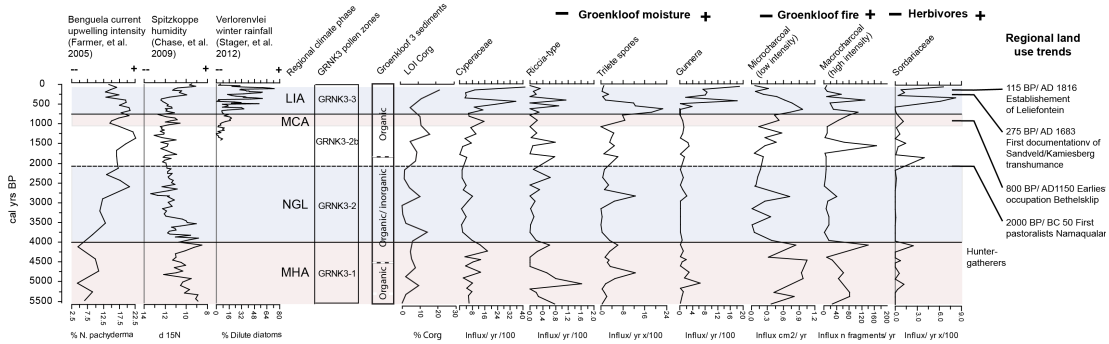

Figure 4.10. Composite diagram showing (from left to right) Benguela upwelling intensity as indicated by abundance of foraminiferan Neogloma pachyderm*a (left coiling) (Farmer, et al. 2005); Humidity indicated by hyrax midden* $\partial^{15}N$ *at Spitzkoppe, Central Namibia (Chase, et al. 2010); Regionally recognised climate phases (MHA = Mid-Holocene Altithermal; NGL = Neoglacial; MCA = Medieval Climate Anomaly; LIA = Little Ice Age); Sedimentological proxies from Groenkloof; Moisture proxies from Groenkloof; Groenkloof fire proxies; Groenkloof herbivory proxies; Kamiesberg land-use history, derived from Webley (2007).*

There is evidence in the Groenkloof record that temperatures decreased around the transition between the MHA and neoglacial phases. Local temperature change is indicated by changes in the abundance of the frost intolerant taxon *Gunnera perpensa*. Its influx is high prior to 4,000 cal yrs BP, after which it is absent for approximately the following 1000 cal yrs BP, suggesting local conditions were indeed warmer at Groenkloof during the MHA (Glen, 2005; Figure 4.10). Further indictor taxa in the Groenkloof record provide evidence of local climatic conditions. Moisture indicators Cyperaceae, *Riccia*-type (van Geel, et al. 1983), Zygnemataceae (van Geel, et al. 1980) and *G. perpensa* are all significantly more abundant in the earlier zone than in the latter. This evidence suggests that the MHA termination was characterised a reduction in moisture availability and temperature at Groenkloof (Figure 4.10). Sedimentological evidence also broadly suggests the lower phase was wetter than the upper, with a higher and more extensive organic carbon component in the lower portion. The upper phase is characterised by a higher minerogenic (sand) component (Figure 4.10). The record at Groenkloof therefore appears to suggest that regionally warmer climatic conditions associated with the MHA were contemporaneous with warm, mesic local conditions and prevalent fire, and that onset of the neoglacial cool phase at 4,000 cal yrs BP coincided with a cooler, drier climate at the site.

This palaeoclimatic pattern at Groenkloof contrasts strongly with palaeoenvironmental records from the south western Cape and Cederberg that indicate the MHA termination and onset of the neoglacial was characterised by wetter conditions from 4,000 years BP (Carr, et al. 2006; Chase and Thomas, 2007a, b; Meadows, et al. 1996; Meadows and Baxter, 2001; Quick, et al. 2011; Scott, 1994; Scott and Woodborne, 2007; Valsecchi, et al. 2013). These wetter conditions at more southerly distributions likely resulted from increased intensity of the winter rainfall-bearing westerlies and a decreased intensity of the South Atlantic Anticyclone as Holocene temperature decreased (Chase, et al. 2013; Cockroft, et al. 1987). In contrast, records toward the north of this axis, where Groenkloof is located, show an inverse relationship, cooling following the MHA being associated with indications of decreased moisture (Chase, et al. 2009; 2010; Scott, et al. 1991). This is consistent with northward deflection and increased intensity of the South Atlantic Anticyclone (SAA), which is reflected in increased Benguela upwelling intensity (Farmer, et al. 2005; Figure 4.10). Increased influence of the SAA caused reduced moisture in Namibia by restricting easterly flow from the summer and year-round rainfall zones (Chase, et al. 2009; Eitel, et al. 2002; Stute and Talma, 1997; Figure 4.10). The contrasting relationships between precipitation and aridity at northerly and southerly distributions of western southern Africa, and the aridification observed in the Groenkloof record, can therefore be explained by changes in the positions and intensities of the winter and summer rainfall zones and their respective circulation systems.

Groenkloof is located at around mid-latitude with respect to the south western Cape and Namibia (Chase and Meadows, 2007), and is positioned close to boundary of the winter rainfall zone (WRZ) and year-round rainfall zone (YRZ) systems. Palaeoenvironmental records from this part of the region are few and sparse, and this study therefore offers valuable insight into fluctuations in the position and nature of regional climatic systems. It is proposed here that a poleward contraction of the westerlies during the MHA would lead to a reduced influence of the South Atlantic Anticyclone (SAA) on climate in the Kamiesberg. This would result in reduced intensity of summer aridity through increased easterly flow and convective rainfall in

summer. Following the onset of the neoglacial, northerly deflection of the westerlies and SAA would reduce easterly flow and intensify seasonal aridity in the Kamiesberg.

Charcoal reductions of both size classes indicate that fire decreased in prevalence substantially at Groenkloof at the 4,000 cal yrs BP boundary (Figure 4.10). Increased aridity would reduce biomass production and fuel for fire (Daniau, et al. 2012). Reduced frequency of lightning events associated with summer rainfall following the MHA are also likely to have impacted on fire frequency (Keeley, et al. 2012). Given the sparse, patchy nature of flammable vegetation in the Kamiesberg (Anderson, 2008; Rebelo, et al. 2006) frequent lightning storms are an important ignition source. Therefore a combination of increased aridity and reduced chance of ignition would have contributed to the reduced charcoal influx following transition from the MHA to neoglacial at Groenkloof.

Interestingly, MacKellar, et al. (2007) modelled rainfall for Namaqualand based on interpolated historical weather station data between 1950-1999 and show increased summer rainfall to the north-east of the region. Further, multi-model projections for the 21st century suggest that late summer convective precipitation in this region will increase. Winter drying in coastal regions however is projected to increase consistent with poleward contraction of the mid-latitude westerly cyclones under warming climate. These model results for historical and future climate scenarios are thus consistent with the geographic patterns of change described above - specifically drier MHA conditions in areas in strong geographical association with the present WRZ, and more mesic climate with increased summer precipitation and lightning closer to the YRZ. In the future, then, we might expect a decrease in summer moisture stress in the Kamiesberg.

4.2.2. Zone GRNK3-1 to GRNK3-2a (5535-2130 cal yrs BP): Ecological Impacts

From 5535 to 4,000 cal yrs BP, during the warm MHA, fynbos taxa and fire dominate the pollen spectra (Figure 4.11). The phase characterised by some of the warmest temperatures in the present interglacial were characterised by some of the highest abundances of fynbos recorded at Groenkloof. It has long been suggested that

interglacial climatic refugia are required in order to account for the apparent antiquity of some fynbos evolutionary lineages (Bakker et al. 2005; Deacon, et al. 1992; Dynesius and Jansen, 2001; Jansen and Dynesius, 2000; Linder, et al. 2005). Verboom, et al. (2009) suggest that, based on the present geographical concentration of palaeoendemic species (Linder, et al. 1992), the moister, cooler, less seasonal environments of the Cape Fold Mountains south of the Great Escarpment may have acted as long-term fynbos climatic refugia through not only the Quaternary but possibly the entire Cenozoic. The palaeoclimatic mechanism described above likely ensured refugial microclimatic conditions suitable for fynbos persistence through the warmest parts of the present interglacial because increased summer rainfall would buffer the effects of higher temperatures on plant available moisture, and perhaps through others with even warmer interstadial conditions, such as marine isotope stage 5e of the Eemian (the 'Last Interglacial') (Quick, et al. 2015). The climatic mechanisms described above supports strongly the suggestion that upland habitats in the fynbos biome have been climatically buffered by summer moisture deliver in warm phases.

From 4,000 cal yrs BP, fynbos becomes markedly less abundant relative to the other pollen groups. Proportionally it dropped from around 90 % to 55 % at 4045 cal yrs BP, and thereafter fluctuates rapidly between 80 and 50 % reaching minimum abundance at around 2,000 cal yrs BP (Figure 4.11). Charcoal deposits were greatly reduced after the transition, particularly between 4,000-3,000 cal yrs BP. The majority of this decrease in fynbos seems to be accounted for by Muraltia, with other dominant taxa (Cliffortia, Stoebe-type and Anthospermum) maintaining comparable abundances. Cliffortia actually increases following this shift (Figure 4.11). These shifts coincide with decreased temperature, increased aridity and a strong reduction in fire (discussed in section 6.1, above).

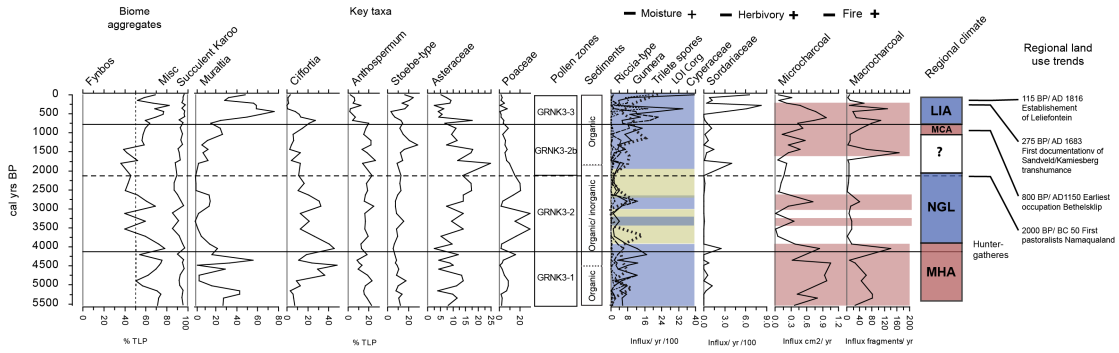

Figure 4.11. Ecological summary diagram for Groenkloof 3. Shown are (from left to right) biome aggregate data; key pollen taxa; pollen zones; sediment profile; moisture proxies; herbivory proxies; fire proxies; regionally recognised climate phases (MHA = Mid-Holocene Altithermal; NGL = Neoglacial; MCA = Medieval Climate Anomaly; LIA = Little Ice Age; ? = no recognised phase); Kamiesberg land-use history, derived from Webley (2007).

Muraltia is common in fynbos in the early post fire stage and can dominate where fire frequency is high (Saunders and Saunders, 2000). Members of the genus show strong adaptations to fire including fire-stimulated seedling recruitment (Keeley and Fotheringham, 2000; Tormo, et al. 2014) and are possibly nitrogen fixers being closely related to Fabaceae (W. Bond, pers. comm.). The genus *Cliffortia* contains an estimated 60 species that reproduce via seed following fire (obligate seeders). Another 60 germinate independently of fire and are also adapted to fire-prone ecosystems by re-sprouting (re-sprouters/ facultative seeders) (Keeley, et al. 2011). The former type are dependent on fire for recruitment, while the latter are not, making obligate seeding advantageous where fire is guaranteed, but less favourable where fire is limited (Ojeda, et al. 1998). Facultative seeders also possess a range of physiological traits that make them better suited to highly seasonal, moisture limited environments including high resistance to xylem cavitation (Skelton, et al. 2015). The change at 4,000 cal yrs BP at Groenkloof from *Muraltia/ Cliffortia* to *Cliffortia* dominated fynbos therefore likely reflects a shift from a mixed obligate seeder/ facultative seeder to a facultative seeder community in response to reduced fire activity.

Fynbos is widely acknowledged as being susceptible to drought relative to succulent karoo (e.g. Jacobsen, et al, 2009; Vendramini, et al. 2012), and it has been suggested that fynbos species outcompete those of succulent karoo through relatively rapid

growth rates where moisture is not limiting to the former (Lechmere-Oertel and Cowling, 2001). *Cliffortia ruscifolia*, for example, has been shown as less tolerant of aridity stress succulent karoo shrubs (Jacobsen, et al. 2009), and *Elytropappus rhinocerotis* is known to occupy the intermediate climate space between succulent karoo and fynbos in mountainous areas of the Cape Floristic Region (Agenbag, et al. 2008; Rebelo, et al. 2006). Increased aridity at 4,000-2120 cal yrs BP was sufficient to reduce fire prevalence to some extent; however this increase does not seem of sufficient magnitude to exceed the drought tolerance of most of the key fynbos taxa.

Other palaeoecological records for mountains areas of the fynbos biome have been resistant to environmental change through the Holocene at the between biome scale (Quick, et al. 2011; Valsecchi, et al. 2013; Meadows and Sugden, 1991, 1993; Scott and Woodborne, 2007a, b) (Quick, et al. 2011; Valsecchi, et al. 2013; Meadows and Sugden, 1991, 1993). Valsecchi, et al. (2013) recoded taxonomic overturning at De Rif in the Central Cederberg in response to changes in climate and fire which acted to maintain resistance. Thus, similarly to at Groenkloof, fynbos has widely been shown as buffered against environmental change extrinsically by regional climatic buffering, and intrinsically by functional diversity and taxonomic overturning. In many Quaternary pollen records from the GCFR, such buffering has not been clear due to often low taxonomic resolution where functional overturning may have occurred within taxa. However, the generic level processes identified here between *Cliffortia* and *Muraltia* clearly capture the importance of functional diversity in fynbos resilience.

Burning tends to be inhibited in fynbos at around MAP 200-300 mm, which roughly correlates with the climatic isohyet of the fynbos-succulent karoo ecotone (Rebelo, et al. 2006). The lower limit of fire prevalence in Mediterranean-type ecosystems worldwide is also generally around MAP 300 mm (Keeley, et al. 2012). This supports the view that fynbos (or at least some taxa – particularly those that can reproduce independently of fire) may be more resilient to drought than expected (Skelton, et al. 2015; West, et al. 2012).

Fire is highly destructive in succulent karoo, and it has been proposed that fire inhibits expansion of succulent karoo into fynbos (Bond and van Wilgen 1996; DeBano, 1998; Wilson, et al. 2015). Almost no immediate response is recorded among the succulent karoo taxa to substantially decreased fire prevalence and fynbos abundance at the 4000 cal yrs BP transition. Only a slight increase begins to occur around 3,000 cal yrs BP reaching a maximum of 10 % by 2000 cal yrs BP (Figures 4.10, 4.11). One possible explanation for the lack of succulent response is that succulent species are poorly represented in the pollen record. Succulent taxa are commonly insect pollinated, producing fewer, larger pollen grains than many wind-dispersed taxa, (Meadows and Sugden, 1993) therefore they may be less likely to occur in the pollen record than, for example, *Cliffortia*, which produces large amounts of pollen and is a common feature of fynbos pollen diagrams (e.g. Scott and Woodborne, 2007). However, studies of modern pollen-vegetation relationships in the central Cederberg (Meadows and Sugden, 1991, 1993) have shown that surface sediment samples from patches of fynbos and succulent karoo are floristically distinct, indicating that this is a reliable feature of the pollen record. The lack of/ slow response of succulent types indicates that factors other than fire disturbance must have constrained succulent plant abundance at this biome boundary. It is argued here that differing dispersal syndromes and competitive relationships might account for the lack of succulent response.

Following 4,000 cal yrs BP Asteraceae and Poaceae both increase notably in abundance, together accounting for 10-20 % in the basal zone to a maximum of 35 % by 2000 cal yrs BP. Asteraceae increases gradually from around 5-20 % between 4,000 and 1900 cal yrs BP. Poaceae increases to 20 % between 3750-3250 and 2600-2000 cal yrs BP, but is almost absent at around 4,000 and 3,000 cal yrs BP. The contemporary ubiquity of the distributions of these taxa (of both plants and pollen rain) (Urrego, et al. 2015) make specific ecological interpretations of this trend problematic. However some indication of its significance relevant to this study can be inferred.

Grasses are apparently never abundant at the same time as Mesembreanthemum (Aizoaceae) (Desmet, 2007). Shiponeni, et al. (2011) demonstrated that under conditions of moisture stress the C_4 grass Stipagrostis brevifolia, outcompetes

common succulent karoo shrubs Ruschia robusta and Leipoldtia pauciflora. Both types possess similarly shallow rooting depths and so are in direct competition for nutrients and moisture. C_4 grasses require summer rainfall (Talma and Vogel, 1992) and their abundance is thus not compatible with cooling regional environmental conditions. However, C_3 grasses also tend to have shallow rooting systems (Fowler, 1986), and may therefore have outcompeted succulents in colonising bare ground. Although grasses in general are very rare in the succulent karoo at present (Desmet, 2007) this in not true of the fynbos-succulent karoo transition at Groenkloof and in the Kamiesberg more generally, where perennial species of the taxa Danthonia, Ehrharta, Chaetobromus, Finicia, Fingerhuthia and Schismus can become abundant across the transition zone (Mucina, et al. 2006).

Both Kamiesberg Granite Fynbos and Namaqualand Granite Renosterveld are asteraceous, which is typical of arid fynbos (Campbell and Werger, 1987; Cowling, 1997; Rebelo, et al. 2006). At present, fynbos at Groenkloof is dominated by taxa such as Eriocephalus africana, Metalasia densa and Chrysanthemoides monilifera, which dominate south and east facing slopes. These taxa are widespread across the GCFR and further across other southern African biomes. They mostly occur on well-drained, sandy soils or rocky habitats, and are pioneers capable of colonising sparsely vegetated habitat (van Jaarsveld, 2001). Other common Asteraceae taxa when surveyed included *Pentzia, Arctotheca, Gazania*, and *Dimorphotheca*, all of which were more common in Groenkloof on more arid north facing slope or very rocky terrain with skeletal soils. They are similarly widespread in the GCFR, but are perhaps more associated with Namaqualand's spring floral displays. It might be therefore that the increased proportion of Asteraceae represents a mixture of generalist types presently associated with more arid fynbos or succulent karoo.

In the contemporary Namaqualand and the Kamiesberg environment, prominent early spring floral displays dominated by annual Asteraceae occur in response to strongly seasonal winter rainfall climate (Cowling, et al. 1999). While these are noted to occur on ruderal ground such as rangelands and abandoned farmland, they also occur where physical stress inhibits the development of perennial plants (van Rooyen, 1999). The likely decline in fynbos biomass associated with increased aridity in the neoglacial

presumably resulted in greater inter-plant spacing and thus provided habitat for annuals to proliferate. Succulent plant species generally lack traits that promote long distance dispersal (Midgley and Thuiller 2007; van Rheede, van Oudtshoorn and van Rooyen, 1999), whereas seed dispersal and production is likely to be higher in annuals (van Rooyen, 1999). The low magnitude and pace of response of succulent karoo shrubs may therefore reflect poor ability of succulent karoo to colonise new environmental space opened-up by stress-induced decline in the fynbos community. This ecological opportunity may in part to have been filled by annual Asteraceae displays typical of today. This supports the suggestion (Desmet, 2007) that the spring annual displays are not a recent phenomenon associated with high intensity agriculture, but that Namaqualand's flora evolved with a long history of disturbance.

4.2.3. Zones GRNK3-2a to GRNK3-2b (4,000-740 cal yrs BP to near present): Palaeoenvironmental Context

Around two thousand years ago mesic indicators Cyperaceae, Riccia-type, Gunnera and trilete fern spores make a resurgence (Figure 4.10). Deposition of the uppermost sediment unit of organic peats occurred shortly after, initiating by around 1800 cal yrs BP. This may be a manifestation of aridity associated with the neoglacial, which is roughly defined as 4,000-3,000 cal yrs BP (Talma and Vogel, 1992). This is supported by a persistent resurgence in Riccia-type from 3,000 cal yrs BP at this time. However, it is not until about 2130 cal yrs BP that all moisture loving indicator taxa re-emerge in the record. This date is therefore taken as reflective of a change in the local environment. Charcoal influx increases even later, at around 1,500 cal yrs BP. This variability among the palaeoenvironmental indicators suggests that the neoglacial termination was both gradual and variable. At around 1000 cal yrs BP, coincident with the onset of the Medieval Climate Anomaly (1000-750 cal yrs BP/ AD 950-1250) (Nicholson, et al. 2013) there are further indications of more mesic, biologically productive conditions, though this does not appear as a pronounced event; rather as a continuation of warming associated with amelioration of the neoglacial. The MCA is not consistently expressed in southern Africa (Nicholson, et al. 2013), and it seems that the ecological response to neoglacial cooling was more significant at Groenkloof. The hydrological changes indicated in both these phases are nonetheless subtle in comparison to those at the MHA-neoglacial transition.

The transition from GRNK3-2a to GRNK3-2b was delimited by an increase in the abundance of spores of coprophilous fungi Sordariaceae (rather than statistical modelling), which are indicative of increased large herbivore abundance (Baker, et al. 2013). Native ungulates of Namaqualand (those present prior to the immigration of domestic stock) were predominantly mixed grazer/ browsers including springbok (Antidorcas marsupilais), gemsbok (Oryx gazelle), steenbok (Raphicerus campestris), grey duiker (Sylvicapra grimmia), klipspringer (Oreotragus oreotragus) and hartebeest (Alcelaphus buselaphus) (Orton and MacKay, 2008). These species are capable of obtaining adequate moisture from vegetation and are thus independent of open water sources, which is a general characteristic of the wild ungulate fauna of the western portion of southern Africa now and during the Holocene (Faith, 2011; Hempson, et al 2015). It is thus unlikely these animals congregated at water sources which might expose them unnecessarily to predation (e.g. by hunter-gatherers, leopard (Panthera pardus)) and their dung would not then be represented strongly in the Groenkloof 3 record.

The increase in Sordariaceae spores occurs broadly coincident with the earliest evidence of pastoralism in South Africa around two thousand years ago, when a new population of people migrated south into Namaqualand (Sadr, 2015). These were likely hunter-gatherers with limited numbers of livestock (sheep and/ or goats) (Orton and MacKay, 2008). Diffusion of pottery and other cultural artefacts across regional archaeological sites suggests geographical mobility (Webley, 2007). Seasonal transhumance patterns of pastoralists to the uplands in summer when lowland sites became desiccated would likely have focussed on areas of key resource availability with water and vegetation suitable for animal fodder. Mesic sites such as Groenkloof would therefore have become focal points of activity for the pastoralists. This means that the impacts of large herbivores around the site would have increased from zone GRNK3-2a to GRNK3-2b at around 2130 cal yrs BP.

4.2.4. Zones GRNK3-2b to GRNK3-2b (4,000 to 740): Ecological Impacts

From around 2,130 cal yrs BP at the onset of zone GRNK2b, the proportion of fynbos increases (largely of Cliffortia and Muraltia). This occurs gradually though the zone,

and contrasts with a gradual decrease in the proportion of Poaceae and Asteraceae (Figure 4.11). It may well be therefore that, as the neoglacial eased in its intensity (Talma and Vogel, 1997), summer aridity decreased which afforded a competitive advantage to fynbos species over arid adapted members of Poaceae and Asteraceae (see Lechmere-Oertel and Cowling, 2001). Further, increased fire indicated by a resurgence of charcoal deposits would have favoured a return in fire prone fynbos taxa and suppressed growth and establishment of fire-sensitive, arid adapted Poaceae and Asteraceae.

The introduction of livestock to the region associated with Khoi pastoralists (Orton 2012) and selective feeding on Asteraceae and Poaceae over fynbos may also account for this shift, particularly if these taxa do represent herbaceous annuals that would be very palatable. A similar reduction in grassiness at around 1,800 cal yrs BP in the south western lowlands around Elands Bay has been tentatively attributed to a land-use change (Meadows, et al. 1996; Meadows and Baxter, 2001). In palaeo- records across southern Africa in the late Holocene, disentangling climate and land-use drivers of ecosystem change is often problematic (Sadr, 2015). This may be symptomatic of the close relationship between people, their land-use practices, climate change and ecosystem dynamics. It is not possible to disentangle these drivers here, but it can be suggested that climate and land-use change interacted to alter ecosystem dynamics. Any human impact was however subtle at this time. Climate, it seems, was also not particularly forceful, the MCA not seeming to coincide with any prominent vegetation changes apart from a continuation of those associated with warming as the Neoglacial eased (Figure 4.11).

Up to this point in the record, no distinct groupings of samples emerge from the NMDS analysis of the Groenkloof data (Figure 4.12) suggesting that no ecological thresholds have been crossed (Holling, et al. 2002). The system responded closely to climate, albeit via, and its long-term resilience is ultimately determined by geography. Such systems are typical of arid environments, whereby moisture becomes so limited that climate and closely related processes (e.g. fire) tend to dominate dynamics Brown 1995; Darwin, 1859; Dobzhansky 1950; Louthan, et al. 2016; MacArthur 1972; Merriam, 1894; Schimper, 1903; Walter, 1971; von Humboldt, 1807).

4.2.5. GRNK3-3 (740 cal yrs BP to near present): Palaeoenvironmental context

The most pronounced influx of hydrophilic indicators taxa in the entire record occurs contemporaneous with the Little Ice Age (LIA). From 740 cal yrs BP to near present, there is a marked increases in fern spores, peaking at 595 cal yrs BP, then declining sharply. Cyperaceae, Riccia-type and Gunnera also peak prominently but do so later at 520 cal yrs BP, where after these taxa also decline sharply (Figure 4.10). The Little Ice Age (LIA) has been defined in southern Africa as 650-100 cal yrs BP (AD 1300-1850) (Nicholson, et al. 2013; Matthews and Briffa, 2005; Jones, et al. 2001), and is more consistently expressed than the MWP across southern Africa (Holmgren, et al. 2003; Lee-Thorp, et al. 2001; Huang, et al. 2000; Talma and Vogel, 1992; Tyson and Lyndesay, 1992). It is generally characterised by cooler temperatures than present (Nicholson, et al. 2013) and appears to be the most extreme cold excursion in the Holocene (Weldeab, et al. 2013). At first, cooling and wetting at the LIA seems paradoxical, given the nature of the warm/ mesic, cool/ arid relationships identified in lower portions of the record. However, examination of the mechanics of the broader environmental context of these changes provides a clearer understanding of their nature.

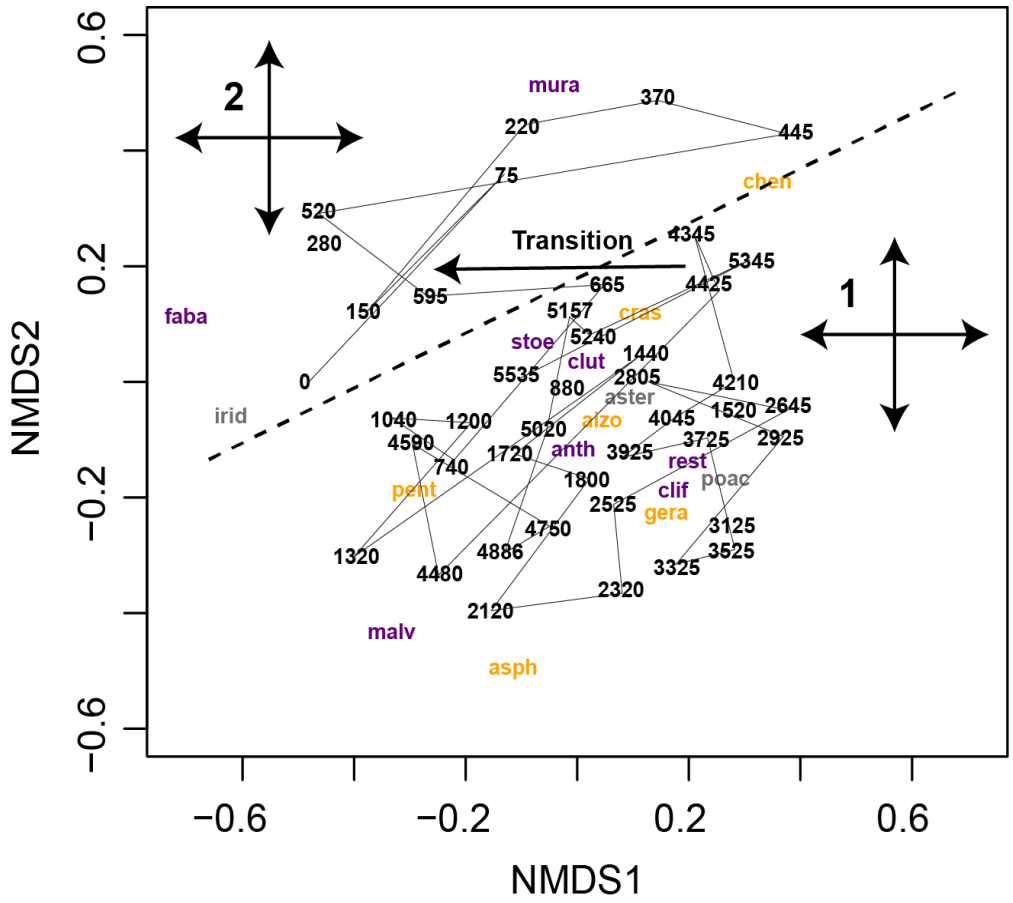

Figure 4.12. Groenkloof NMDS with interpretation of system resilience. Only dimensions 1 and 2 revealed the state shift. Arrows reveal directions of change in the system. State 1 is multi-directional resulting from close tracking of climate and fire with weak feedbacks. The transition to state 2 appears to have been unidirectional (i.e. potentially non-reversible).

Around the time of the Last Glacial Maximum (~25,000 cal yrs BP), the winter rainfall zone was enhanced and expanded to the north and east in southern Africa due to propagation of Antarctic sea ice and resulting latitudinal shifts in atmospheric circulation systems (Chase and Meadows, 2007). Last Glacial Maximum temperatures were on average around 6oC lower than today. This is far lower than those of the LIA, which were at most 1-3oC below present. However the same broad mechanism can be invoked to explain increased moisture availability in Groenkloof 3 contemporaneous with the LIA. At Verlorenvlei on the west coast of South Africa (Stager, et al. 2012), inferred rainfall increased markedly from around 700 to 20 cal yrs BP. Similarly, Benito et al. (2011) recorded an increase in the occurrence of large flood events of the Buffels River from around 525 to 25 cal yrs BP (AD 1425 to 1925). The catchment of the river drains the Kamiesberg and therefore likely reflects

a very similar palaeohydrological history. Off the coast of Namaqualand, Weldeab, et al. (2013) recorded wetter conditions during the past 600 cal yrs BP than background Holocene conditions. This evidence therefore suggests that LIA wetting was widespread regionally, and numerous authors (Benito, et al. 2011; Chase, et al. 2013; Stager, et al. 2012; Weldeab, et al. 2013) have attributed this to increased Antarctic sea ice and the resulting enhancement and expansion of the austral westerlies.

Webley (1986) produced archaeological evidence demonstrating that pastoralists occupied the Kamiesberg seasonally around this time. The earliest dated site is at Bethelsklip some 30 km east of Groenkloof in the arid Nuwerus Valley. Dung, ash heaps, and stockposts are have been identified, the oldest of the latter having been dated to 735 ± 75 cal yrs BP, which overlaps with the transition to zone GRNK3-3 at around 740 cal yrs BP. Webley (1986, 2007) argues that these pastoralists migrated between the lowlands and uplands seasonally to optimise resources and avoid heat/ cold in summer/ in winter, respectively. The Little Namaqua are known to have burned fynbos to stimulate growth of geophytes, the shooting bulbs of which would provide a dietary carbohydrate source the following summer. Thus, while climate change at this time was particularly pronounced, archaeological evidence suggests the time was also associated with unprecedented land-use intensity.

4.2.6. GRNK3-3 (740 cal yrs BP to near present): Ecological context

Muraltia dominates the pollen spectra in zone GRNK3-3, peaking at around 70 % of the pollen rain by 450 cal yrs BP (Figure 4.11). As discussed above, *Muraltia* is common in fynbos in the early post fire stage. It is fire dependant and can dominate where fire frequency is high. During the MHA fire frequency was high due to the combination of high biomass and frequent ignition, where increased easterly flow in summer resulted in reduced summer aridity and increased lightning. During the LIA, however, rainfall in the Kamiesberg was strongly seasonal and delivered in winter (Benito, et al. 2011; Stager, et al. 2012; Weldeab, et al. 2013). Lightning in the fynbos biome has been shown to be more common under summer rainfall conditions, predominantly due to heightened humidity (Kraaij, et al., 2013a). Frequent-fire loving Muraltia might therefore be expected have been more abundant within conditions of

the MHA than the LIA. This is not the case. During the MHA vegetation was dominated by herbs (Muraltia) graminoids (Restionaceae, some Poaceae) and woody shrubs (*Cliffortia, Stoebe*-type, *Anthospermum*), while the LIA was dominated by herbaceous *Muraltia* with some *Stoebe*-type shrubs (Figure 4.11). This indicates high biomass fires in the MHA as opposed to low biomass, very frequent fires in the LIA. So why were fires more frequent in the LIA compared to the MHA?

The answer may be people. By promoting burning of fynbos to stimulate growth of carbohydrate-rich geophytes (Webley, 1986; 2007), Little Namaqua during the LIA may have performed a similar ecological functional role to summer lightning in the MHA - fire ignition. There are however some important differences in the plant community resulting from this new anthropogenic ecology.

Having been remarkably stable through the preceding portion of the record Anthospermum rapidly declines in abundance after 740 cal yrs BP (AD 1200) (Figure 4.11). Species of this genus in the fynbos biome (e.g. *A. spathulatum*) are known to be particularly palatable and decrease substantially as grazing intensity increases (Milton, 2007). Its sudden decline may therefore reflect the impact of pastoralists and their livestock using Groenkloof as a summer refuge (see Webley, 2007). Increased grazing intensity therefore seems to have modified the ecosystem away from the ecological potential that mesic climate of the LIA may have afforded.

A decline in *Stoebe*-type is focussed around 450 cal yrs BP. *Stoebe*-type contains two indistinguishable genera – *Stoebe* and *Elytropappus* (Scott and Woodborne 2007). In the present-day Kamiesberg vegetation, *Stoebe* is not noted as important nor abundant (Rebelo, et al. 2006) and was not recorded as occurring at Groenkloof in analysis of the present vegetation (Appendix 1). The pollen taxon is therefore assumed to represent predominantly *Elytropappus rhinocerotis*. The species is highly drought tolerant; reproduces from seed in abundance rapidly following fire and is thus tolerant of all but the shortest fire regimes; forms dense stands which suppress competitors; and is also unpalatable typically becoming abundant on heavily grazed sites (Proksch, et al. 1982; Keeley et al. 2012; Levyns, 1926). The fire return period at around 450 cal yrs BP must therefore have been exceptionally short (< 4 yrs) to suppress

abundance of *E. rhinocerotis*. *Cliffortia* similarly declines substantially, being almost absent in the upper portion of the zone and to the surface. This suggests exclusion of obligate seeders under high fire frequencies.

It therefore appears that the dual pressures of grazing and high fire frequency (the former possibly associated with climate-induced changes in pastoralism) altered the system at Groenkloof to an alternative stable state (Holling, et al. 2002; Scheffer, et al. 2001) following 740 cal yrs BP, whereby land-use disturbance characteristics determine an alternative pathway to that dictated by climate alone. Herbivory and fire modified the system away from palatable *Anthospermum* towards dominance of fire-loving *Muraltia*. Once established the dominance of fire-loving woody shrubs and herbs maintained their dominance through out shading (see Hoffmann, et al. 2012) and promoting high fire frequencies and intensities (Burger and Bond, 2015) that are destructive to all but the most disturbance-adapted species. An ecosystem shift is evidenced in the NMDS plot around this time reflecting simplification of the community towards heavy-disturbance adapted *Muraltia*, *Elytropappus rhinocerotis*, as well as some ambiguous members of Fabaceae and Iridaceae, associated with increased human activity. While earlier in the record the fynbos-succulent karoo ecocline at Groenkloof acts in a 'fluid' way, with biome distribution resembling Gleasonian individualist organisation in response to climate change, under heavy land-use pressure the system became more Clementsian with stronger system cohesion and feedback control.

4.3. GROENKLOOF 3 ENVIRONMENTAL AND ECOLOGICAL SUMMARY

Under climatic conditions warmer than today during the Mid Holocene Altithermal (MHA) (Talma and Vogel, 1997), fynbos and fire dominated at Groenkloof (Figure 4.13), with a low representation of succulent karoo taxa. The community was mixed, containing a diverse array of functional types with different response traits in relation to stress, competition and disturbance. Increased aridity and cooling subsequently occurred at around 4,000 cal yrs BP between the MHA and Neoglacial at Groenkloof, likely due to the site's proximity to the year-round rainfall zone and the effects of climatic cooling on regional atmospheric circulation (Chase, et al. 2010). This

reduced fire at Groenkloof by limiting biomass production and ignition by lightning, which resulted in an overall decline in fynbos abundance though only fire-responding *Muraltia* was lost from the pollen spectra. This primarily reflected decreases in fire-dependent functional types. Typical fynbos taxa that reproduce independent of fire persisted and even proliferated, apparently unhindered by pronounced aridity, suggesting high resilience to drought.

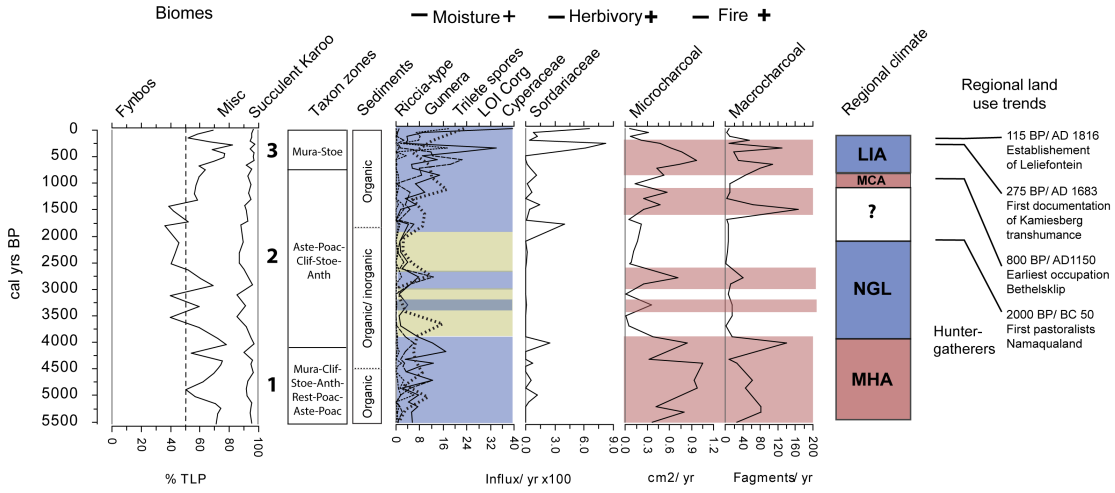

Figure 4.13. Summary of biome characteristics recorded in the Groenkloof 3 record. From the left, the relative biome abundances; taxon zones (or ecosystem states) indicate statistically significant taxon zones identified by CONISS, and the key taxa of the plant community associated with each phase (note the decreasing taxonomic complexity of phases 1-3.) Environmental indicators and variables are towards the right for moisture, herbivory, fire, and regional climate and land-use patterns.

The community that emerged at Groenkloof in response to the MHA-Neoglacial transition (~4,000 cal yrs BP) was not characterised by dominance of 'typical' fynbos nor succulent karoo taxa. Rather, members of the Asteraceae and Poaceae, both considered generalists because of their wide array of ecological affinities, came to dominate the flora (Figure 4.13). The increased proportion of Asteraceae may have been associated with an increase in annual Asteraceae, suggesting that the famous Namaqualand spring blooms are not in fact a recent anthropogenic phenomenon (Cowling, et al. 1999; Desmet, et al. 2007), but rather a drought response and an integral feature of the region's ecological and evolutionary history. Alternatively, generalist species typical of arid fynbos and the ecotone may have proliferated. Contemporaneous increases in the abundance Poaceae are similarly ambiguous, though most likely represent C_3 grasses typical of the Kamiesberg uplands (Mucina,

et al. 2006). Low responsiveness of succulent karoo types to reduced aridity and fire is attributed to differing dispersal syndromes and competitive relationships. Succulents typically produce large seeds or reproduce vegitatively, which is not conducive of rapid or large-scale shifts in population distributions. In contrast, members or Asteraceae (particularly annuals) produce abundant small seeds, making their population distributions more dynamic. As environmental niche space opened-up in response to increased aridity, fynbos productivity decline fire inhibition, this latter group were likely more adept at establishing the empty 'space' (both physical and niche) at the fynbos-succulent karoo ecotone.

As the neoglacial eased from around 2000 cal yrs BP (Talma and Vogel, 1992), summer aridity and associated plant moisture stress decreased and likely afforded a competitive advantage to fynbos herbs and woody shrubs over Poaceae and Asteraceae. This allowed the fynbos community to gradually re-establish (Figure 4.11). Later, around the time of the Medieval Climate Anomaly (MCA; 1000-750 cal yrs BP/ AD 950-1250) (Nicholson, et al. 2013), environmental and ecological changes did occur at Groenkloof, with fynbos continuing to increase; however these trends appear to be a continuation of the neoglacial easing. The MCA therefore did not have a pronounced impact at Groenkloof, which is consistent with regional observations (Holmgren, et al. 2003; Lee-Thorp, et al. 2001; Huang, et al. 2000; Talma and Vogel, 1992; Tyson and Lyndesay, 1992). The MHA may therefore provide more valuable insights as to the effects of future warming.

The Little Ice Age (LIA; 750 to 100 cal yrs BP), perhaps the coldest phase in the Holocene of southern Africa, was characterised by the wettest recorded environments at Groenkloof 3 and in the western region during the present epoch (Benito, et al. 2011; Chase, et al. 2013; Stager, et al. 2012; Weldeab, et al. 2013). This contrasts with conditions expressed during earlier phases of the record, where cooling resulted in drying. The apparent paradox reflects the geographical position of Groenkloof in relation to regional climatic phenomena during Holocene temperature maxima and minima. During the MHA, Groenkloof experienced a positive moisture balance due to increased easterly flow and reduced influence of the South Atlantic Anticyclone. In the LIA, the westerlies system intensified bringing increased winter rainfall reflecting

a similar mechanism to that which occurred around the Last Glacial Maximum (Chase and Meadows, 2007).

Despite winter rainfall being the dominant source of increased moisture during the LIA, pollen of frequent-fire loving Muraltia (Saunders and Saunders, 2002) was more abundant than during the MHA. Moreover, pollen representative of the LIA was less indicative of well developed fynbos stands, suggesting very frequent fires. Rather than lightning, the coincidence of these events with the first evidence of pastoralists in the Kamiesberg around 735 cal yrs BP (Webley, 1986, 2007) suggests that burning by humans may account for such frequent fires and associated changes in vegetation. As such, humans performed a similar functional role to summer lightning in the MHA. However, important differences in the plant community between the LIA and MHA emerged from this new anthropogenic ecology. Increased land-use intensity resulted in reductions in all but the most disturbance-adapted taxa (i.e. to high herbivory, frequent fire), and a functionally and taxonomically simplified alternative ecosystem state (Figure 4.13).

Prior to around 740 cal yrs BP, the ecosystem at Groenkloof responded closely to climate via its strong control on fire prevalence in dryer Mediterranean-type environments (Keeley, et al. 2012), and its long-term resilience is ultimately determined by the topography and geographical position of the Kamiesberg in relation to regional climatic phenomena. Such systems are typical of arid environments, whereby moisture becomes so limited that climate and closely related processes (e.g. fire) tend to dominate dynamics (Brown 1995; Darwin, 1859; Dobzhansky 1950; Louthan, et al. 2016; MacArthur 1972; Merriam, 1894; Schimper, 1903; Walter, 1971; von Humboldt, 1807). Under heavy land-use pressure the system became more Clementsian with strong system cohesion and feedback control (Estes, et al., 2010; Holling, et al. 2002; Holling, 1973; Oliver, et al. 2015; Scheffer, et al. 2001).

5. BETWEEN- AND WITHIN-BIOME CHANGE AT THE FYNBOS-FOREST BOUNDARY

The prevailing view in ecology holds that a combination of perturbations are required to force shifts between alternative stable states (Willis, et al. 2011). The importance of changes in both abiotic state parameters such as moisture and nutrient availability, and biotic/ disturbance state variables including fire and herbivory is also widely recognised (Beisner, et al. 2003; Holling, et al 2002; Holling, 1973; Lewontin 1969; Scheffer, et al. 2001). Such phenomena are documented worldwide from local to global scales in a variety of systems, though it is yet to be understood how persistent or reversible these transformed states are, and whether restoration of state parameters and variables following change will restore the previous state, or whether changes are hysteretic (i.e. irreversible) (Dakos, et al. 2015; Petraitis, et al. 2013). In the face of global change, it is crucial to identify where and when abiotic and biotic factors determine the potential for alternative ecosystem states, and what factors might trigger state shifts (Oliver, et al. 2015; Slingsby, et al. 2014). Conversely, understanding the factors that mitigate against state shifts and maintain systems through resistance to environmental change will assist in managing for resilience and stability (Holling, et al. 2002).

Biomes are said to be major selective biological filters (Crisp, et al. 2009). Their constituents tend to have shared evolutionary histories with similar life-history traits. This subsequently results in alteration of the abiotic and biotic environment to create conditions favourable to their own success (niche construction) (Linder, et al. 2012). This in turn modifies environmental filtering processes and restricts species immigration (Slingsby, et al. 2014). Upon arrival in a recipient community, an immigrant species is confronted with the challenges of the new environment (Potts, et al. 2015). In addition to the genetic, life history and reproductive attributes that facilitate establishment of an initial population, the immigrant must rapidly adapt to potentially novel abiotic, biotic and disturbance regimes. Some level of pre-adaptation is obviously advantageous, therefore lineages derived from areas where conditions similar to the destination environment prevailed are clearly at an advantage

(Verboom, et al. 2014). It should therefore be expected that ecosystem resistance to colonisation is much higher at between- verses within biome scales.

Palaeoecology offers the potential to investigate past invasions ('palaeo-invasions'; Gillson, 2008; Gillson, 2009) and ecosystem state shifts at both between- and within-biome scales (Gillson and Ekblom, 2009; Gil-Romera, et al. 2010; Valsecchi, et al. 2013). The fossil record offers potential to elucidate the long-term processes and interactions governing ecosystem resilience to immigration and state shifts on timescales of decades to millennia. This allows observations to be made across wide environmental gradients expressed in the past that are relevant to future trends (Froyd and Willis, 2008; Willis and Birks, 2008), and so inform possible future change scenarios and help improve understanding of ecosystem vulnerability.

The palaeoecology and evolutionary origins of afrotemperate forest and fynbos are strongly contrasting (Mucina and Geldenhuys, 2006). Forest and thicket have been a consistent and prominent component of the GCFR flora since at least the Palaeogene at ~70 Ma and are its oldest constituent biome (Verboom, et al. 2014). Late-Miocene aridification from around 10 Ma likely acted in concert with prevalent, recurrent wildfires to drive rapid declines in the abundance of mesic, fire sensitive forest elements (DuPont, et al 2011). This process presumably progressed through the Pleistocene leading to repeated extirpations and extinctions as a result of orbitally-forced climatic oscillations. The consistently high light requirements of fynbos taxa, and low light availability in forest, suggest that fynbos and forest have historically been partitioned. Further, fynbos possesses strong adaptations to summer aridity and fire whereas forest does not. Therefore it is suggested that forests persisted in a matrix of fynbos much as in the GCFR at present, with forest dominant in wetter, fire protected areas (Verboom, et al. 2014). These contrasting abiotic, biotic and disturbance environments of the respective biomes are reflected in the strong phylogenetic and biogeographic partitioning of the two biomes (Crisp, et al. 2009; Verboom, et al. 2014). Environments associated with each biome may therefore inhibit between-biome migration though selective filtering based on functional traits associated with life-histories, and biome partitioning should be consistent in space and time.

Contemporary forest expansion into fynbos (Luger and Moll, 1993; Poulsen and Hoffman, 2015) and palaeoecological data which provide evidence of repeated forest transgressions in the regional Quaternary palaeoecological record (Chase and Meadows, 2007; DuPont, 2007; DuPont, et al. 2011; Irving, 1998; Martin, 1968; Quick, et al. 2015; Scholtz, 1986; Shi, et al. 2000) confirm forest must be able to invade fynbos. Coetsee, et al. (2015, 2013) highlight the potential roles of pioneer afrotemperate forest species in acting as 'biotic modifiers' or 'ecosystem engineers' (Linder, et al. 2012). Such taxa alter the abiotic and biotic environment and modify environmental filtering processes creating more conducive conditions for forest to spread at its boundaries with forest fynbos. Hoffmann, et al. (2012) highlight how interactions among climate, resources and plant traits determine critical thresholds separating forested and open landscape states. They identify a 'fire resistance' threshold denoting when individual trees develop sufficient insulation (bark) to prevent death and promote persistence through fire events. Further a 'fire suppression' threshold may be reached when tree canopy cover is sufficient to shade-out fire-prone vegetation and inhibit fire. This subsequently allows establishment of fire sensitive secondary or tertiary forest taxa. Biome switches from fynbos to forest are likely to be more common at sites where resource limitation and fire frequencies are low. This is because both the proximity of the state transition threshold in the basin of attraction and energy available for the state to change would be increased (Beisner, et al. 2003; Holling, et al 2002; Holling, 1973; Lewontin 1969; Scheffer, et al. 2001; Willis, et al. 2011).

This chapter, firstly, explores the resilience of fynbos to invasion by afrotemperate forest at its temperate boundary. The southern Cape forests co-exist with fynbos in the same climate space (Phillips, 1930; Adamson, 1938; Mucina and Geldenhuys, 2006). The two biomes are therefore alternative stable states (Keeley, et al. 2012; Coetsee, et al. 2015). Debate exists as to whether resources (i.e. nutrients, moisture and light) (Coetsee, et al. 2015), fire disturbance (Geldenhuys, 1994), or interactions among these properties (Coetsee, et al. 2015; Hoffmann, et al. 2012) determine the resistance of fynbos to invasion by forest. As forest expansion could have negative consequences for biodiversity in fynbos (Luger and Moll, 1993; Poulsen and Hoffman, 2015) and associated ecosystem services (Slingsby, et al. 2014), it is

important to understand how and why stability is maintained. If biome switches do not occur despite environmental variability, this will provide insight into fundamental understanding of how biome integrity is maintained through internal properties (Coetsee, et al. 2015) that promote resilience through resistance.

Alternative stable states can be characterised by the presence of differing plant functional types, vegetation structure, biomass and percentage cover, as well as by contrasting ecological processes (Anderies, et al. 2002; Beisner, et al. 2003; Gillson and Duffin, 2007) and can occur at both between- and within-biome scales. Literature on such phenomena within the fynbos biome is sparse, and primarily relates to exotic invaders (Allsopp, et al. 2014). Common invasive aliens, such as *Pinus pinaster* and *Acacia mearnsii,* are known to act as biotic engineers in the creation and maintenance of alternative ecosystem states in fynbos, and pose one of the greatest threats to fynbos ecosystem function and biodiversity at present (Slingsby, et al. 2014; Wilson, et al. 2014; Kraaij, et al. 2014). Indigenous species too can act as biotic modifiers and, often associated with a change in land use (Slingsby, et al. 2014), can be protagonists in the development of undesirable and persistent alternative stable states (Gillson, et al., 2008). The second focus of this chapter, therefore, explores the resilience of fynbos to shifts between alternative stable states at the within-biome scale resulting from interactions among climate, fire and land-use change with biota (Linder, et al. 2012). Species dynamics might be more fluid than at the between-biome scale because species evolved within similar environmental and ecological parameters (Potts, et al. 2015). Alternatively, phylogenetic and phytochorological complexity at the within-biome scale (Bergh, et al. 2014; Verboom, et al. 2009) might result in strong environmental and ecological filtering processes.

The following text explores the pre-historic nature of changes in fynbos vegetation at Platbos in the southern Cape, with particular reference to climate, fire and land-use change and alternative stable states. In doing so, interactions among abiotic parameters, environmental filtering and biotic relationships are explored. The chapter begins by presenting sedimentological, geochronological, fossil pollen, charcoal and spore data from a core at Platbos 1. This information is then synthesised to examine

the roles of abiotic and biotic ecosystem properties in determining fynbos resilience at both between- and within-biome scales.

5.1. PLATBOS 1 RESULTS

5.1.1. Platbos 1 Sediment Description

Sediments of the core Platbos 1 are detailed in Table 5.1. Essentially they were composed of 96 cm of highly humified, homogenous peat. An upper and lower portion were delimited at 26 cm depth in the core by decreasing degree of decomposition and darkness of colour. There appeared to be some minor disturbance to the surface of the core likely resulting from the extraction process.

Table 5-1. Description of Platbos 1 sediments.

Depth (cm)	Troels-Smith	Description	Munsel	Colour	Sediment unit
0-26 cm	$Ld^3$3, $Th^0$1.	Well humified peat with some fibrous plant material.	10YR, 3/3.	Dark brown.	PLB1-B
96-26 cm	$Ld^4$4.	Highly humified peat.	10/YR, 2/1.	Black.	PLB1-A

5.1.2. Platbos 1 Chronology and Age Model

Probability distributions for the two AMS radiocarbon dates generated from Platbos 1 are plotted in Figure 5.1., and detailed results are provided in Table 5.2. Both posterior distributions are multi-modal. However, the area under the 2σ probability distribution is high (> 92 %), showing very good agreement between the prior and posterior distributions (i.e. a reliable calibration between radiocarbon and calendar ages.) A basal age for the deposit was determined as 2910 ± 155 cal yrs BP at a depth of 95 cm. Another age of 1410 ± 230 is provided for 55 cm depth.

Pollen of *Pinus* (pine; likely *P. pinaster*) first occurs at 30 cm depth. This value is chosen arbitrarily as a stratigraphic indicator of the first settlement of Europeans Plettenberg Bay at 160 cal yrs BP (c. AD 1790) (though this date may be some years

later, assuming time to establish the plantation). At a depth of 26 cm pine pollen reaches abundances similar to that within the surface sediments and this likely reflects settlement directly on the Platbos plateau between 70-80 cal yrs BP (c. AD 1870-1880). Pollen of exotic *Eucalyptus* also becomes significantly abundant at the same depth. The surface of the core is assigned an age of -50 cal yrs BP (c. AD 2000) (Table 5.2).

The age-depth model for Platbos 1 is displayed in Figure 5.1. Between 2885 and 1390 cal yrs BP average sedimentation rate is modelled as 0.03 cm/ yr^{-1}. A slight decrease to 0.02 cm/ yr^{-1} then occurs for the period 1335 to 160 cal yrs BP (AD 1790), whereupon the rate increases to 0.7 cm/ yr^{-1} until 75 cal yrs BP (AD 1875). The uppermost portion of the core, from 75 cal yrs BP to -50 cal yrs BP (AD 2000) is characterised by much faster average sediment influx in the region of 0.21 cm/ yr^{-1}.

Table 5-2. Details of al ages used in the Platbos 1 age-depth model.

Depth (cm)	Dating method	Calibration data	^{14}C age	Calibrated age ranges (yrs BP)	Mean (95.4 %) cal BP age/ AD for historical dates	Area under probability distribution (%)
0	Biomarker	Historical	-	-	-50/ 2000	-
26	Biomarker	Historical	-	-	75/ 1875	-
30	Biomarker	Historical	-	-	160/ 1790	-
55	AMS 14C	IntCalSH 13	1490 ± 80	1178-1636	1410 ± 230	92
95	AMS 14C	IntCalSH 13	2760 ± 30	2751-3063	2910 ± 155	94

5.1.3. Platbos 1 Cluster Analysis

The maximum number of statistically significant clusters is indicated to be three by the broken stick model (Figure 5.2). These three clusters are indicated on the dendogram in Figure 5.3. Clusters PLB1-1, PLB1-2 and PLB1-3, respectively, incorporate samples dated to between 2970 and 1590, 1500 and 90, and from 60 to -50 cal yrs BP. Boundaries separating these clusters are defined as the mid-points between end members of each adjacent cluster. The clusters PLB1-1, PLB1-2 and PLB1-3 are therefore defined as 2970 to 1545, 1545 to 75, and 75 to -50 cal yrs BP, respectively. The uppermost three samples represent the Platbos plantation phase and

these samples are hereafter excluded from the analysis, meaning that pollen diagrams end at 50 cal yr BP.

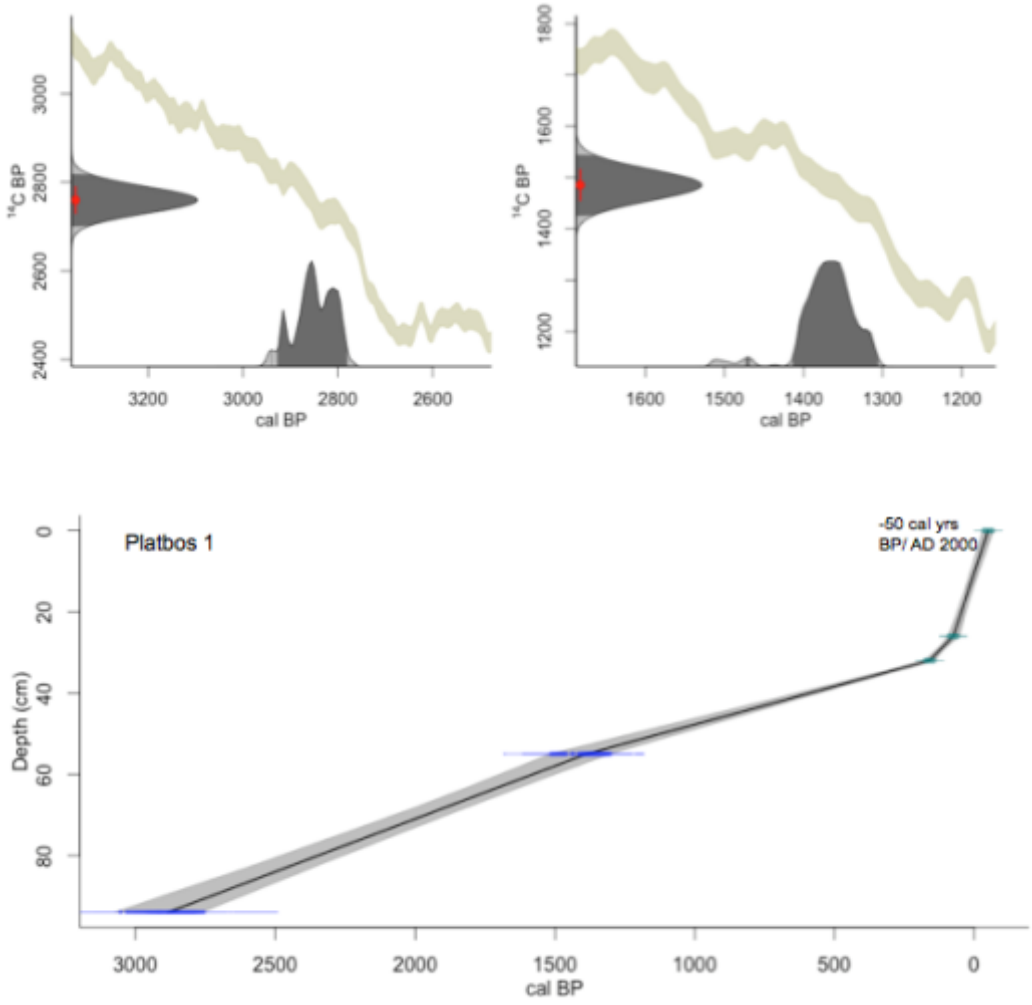

Figure 5.1. Highest posterior density ranges for individual dates from Platbos 1 at 94 cm (top left), PLB2 55 cm (top right), and the age-depth model for the whole core (bottom).

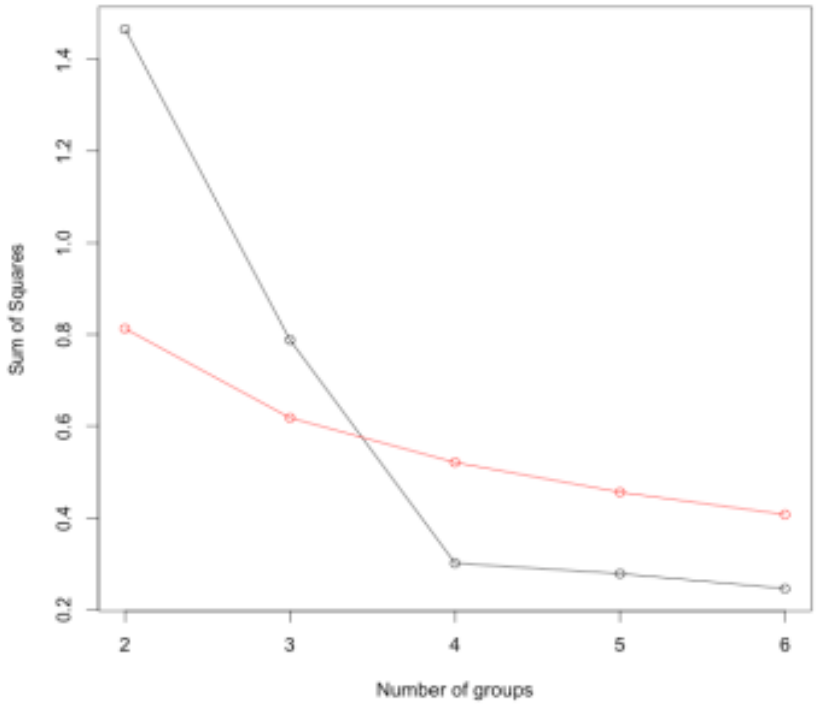

Figure 5.2. Broken-stick model determining the number of statistically significant clusters in the Platbos 1 pollen stratigraphic data. The black line indicates model simulations based on the empirical data, and the red represents random simulations.

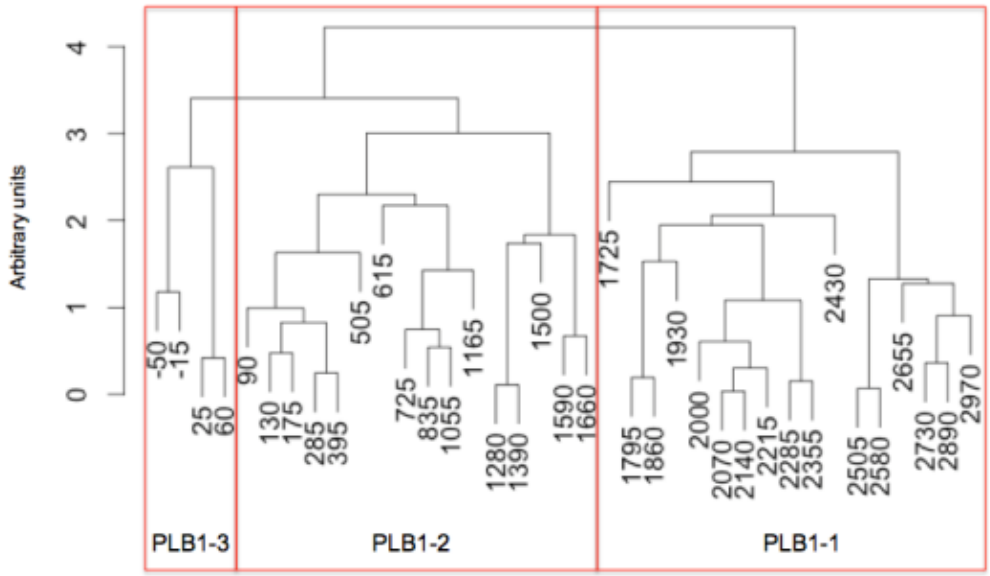

Figure 5.3. Dendogram produced by cluster analysis of the Platbos 1 pollen data with statistically significant clusters separated by red lines.

5.1.4. Platbos 1 Biome Aggregate Data

Figure 5.4. presents the pollen data aggregated into fynbos and afrotemperate forest groups expressed as percentages relative to their cumulative sum. Due to the very low abundance of Poaceae in afrotemperate forest, it is reasonable to assume that Poaceae represents predominantly fynbos species. Through PLB1-1 and PLB1-2 for a period of 2,900 years fynbos pollen dominates, typically constituting 80 % of the sum, the other 20 % being of forest taxa. The amplitude of variation in this ratio of fynbos to forest pollen is only 10 %.

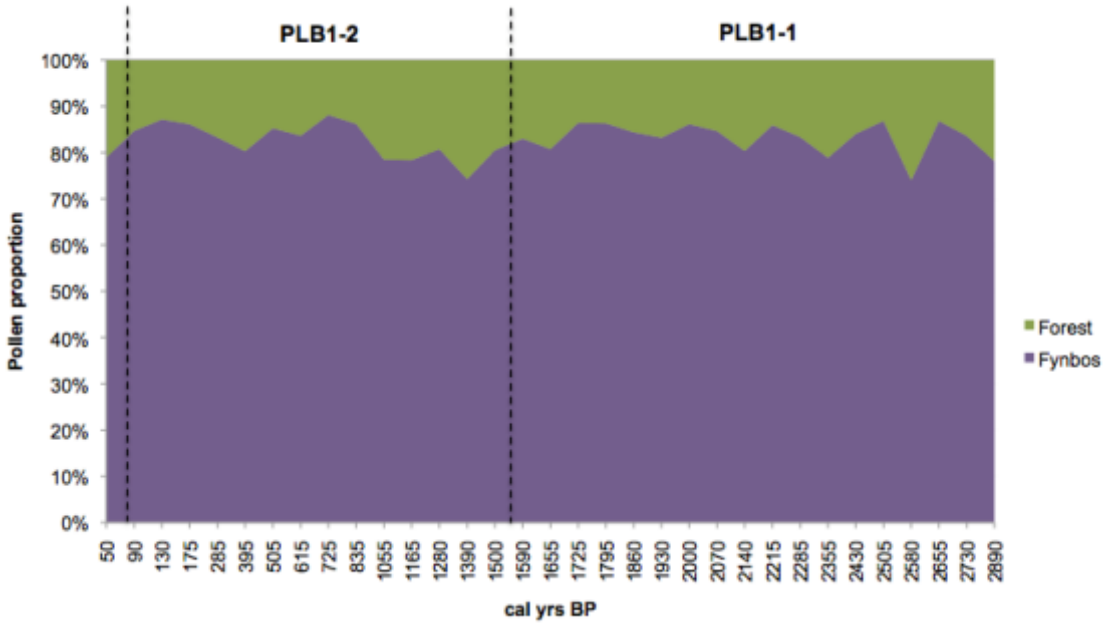

Figure 5.4. Biome aggregates from fossil pollen data from the Platbos 1 core expressed as percentage values. Data are plotted to 50 cal yrs BP as the most recent proportion of the record is distorted by vegetation clearance for establishment of the pine plantation.

5.1.5. Platbos 1 Pollen Diagram.

The Platbos 1 pollen diagram is displayed in Figure 5.5. Only taxa that constituted > 2 % of total land pollen are displayed. Full species lists and accumulation rate data are given in Appendix 2. In cluster PLB1-1 (2970 to 1545 cal yrs BP) the most abundant taxon is *Cliffortia* 1. It is most abundant at the base of the cluster constituting 27 % and declines variably to some 20 % at the top of the cluster. Poaceae is also abundant and fluctuates between 3 % and 15 %. Lower values are more common at the lower and upper portions of the cluster, with intervening peaks at 2430, 2070 and 1700 cal

yrs BP. Higher values occur at 2285, 2000 and 1860 cal yrs BP. Lamiaceae increases in abundance from 4 % at the base of the base of the cluster to 18 % by 1790 cal yrs BP, where after a decline to 6 % occurs. *Berzelia*-type is another important taxon in this cluster. It decreases from 13 % at the base, to 3 % at the top, but with low values (<3 %) centred on 2655, 2430, 2135 cal yrs BP. Restionaceae is low in abundance, typically < 5 % but peaking to 7 % at 2285 cal yrs BP. Ericaceae increases fairly consistently from 3 % to 8 % though the cluster. Asteraceae long spine is abundant between 9 and 17 %, with notable spikes at 2500, 1930 and 1660 cal yrs BP. Proteaceae is present in low abundance in the lower portion of the cluster until 2430 cal yrs BP, where after it is almost absent until 1860 cal yrs BP when it begins to increase reaching 13 % abundance by 1590 cal yrs BP. Other fynbos taxa present but in very low abundance (<5 %) include Crassulaceae, *Passerina*-type, *Anthospermum*, Loranthaceae, Iridaceae and Euphorbiaceae.

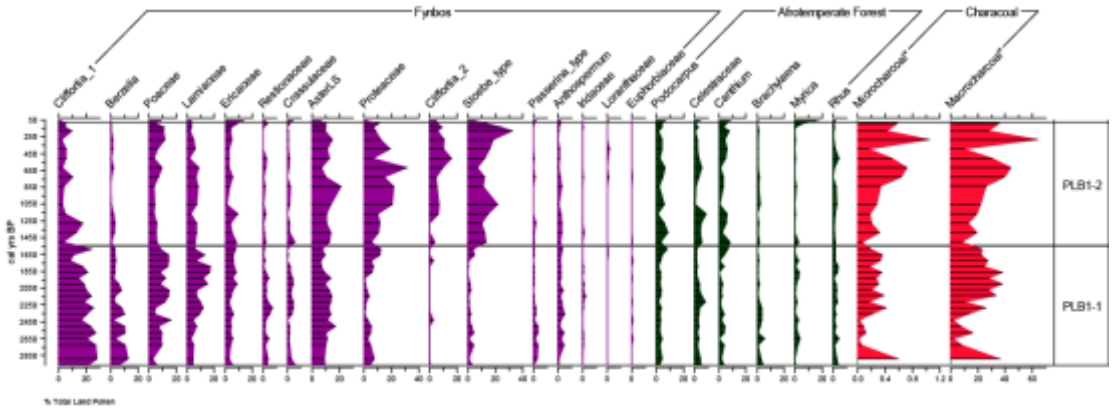

Figure 5.5. Pollen diagram displaying percentage abundances of land-pollen taxa selected on the basis of constituting >2 % of the total land pollen sum (TLP).

Of the forest taxa in PLB1-1, none are very abundant (>10 %) and there are few pronounced trends. A spike in Celastraceae abundance to 8 % can be identified at 2215 cal yrs BP, and both *Podocarpus* and *Canthium* increase to 7 % at the top of the cluster around 1590 cal yrs BP. Other forest taxa present but in low abundance (<5 %) include *Brachylaena*, *Myrica* and *Rhus*.

The superseding cluster PLB1-2 (1545 to 75 cal yrs BP) is characterised by striking shifts in the abundances of fynbos taxa, a number of taxa being less abundant and others proliferating. *Cliffortia* 1 is much less abundant than in PLB1-1, typically

around 5-6 % but with spikes at 1280 (17 %), 725 (10 %) and 175 (9 %) cal yrs BP. Poaceae is less abundant (4 %) from the base of the cluster until 835 cal yrs BP, where after it becomes more abundant to around 7-10 %. Lamiaceae is less abundant than in the preceding cluster, fluctuating around a mean of 5 %. *Berzelia*-type, Restionaceae, Crassulaceae, *Passerina*-type, *Anthospermum*, Iridaceae and Euphorbiaceae are all lower in abundance than in the preceding cluster and are generally scarce comprising < 3 %. In contrast, Asteraceae long spine is more abundant than in PLB1-1, with a notable peak to 21 % at 835 cal yrs BP. The highest Ericaceae abundances on record (5-10 %) straddle the boundary between PLB1-1 and PLB1-2 from 2000 to 1200 cal yrs BP. Strikingly, Proteaceae increases from 5 % at the base of the cluster to a peak abundance of 31 % at 615 cal yrs BP, then declines to 8 %. *Stoebe*-type proliferates from 13 % to 21 % between 1500 and 1060 cal yrs BP, declines to 7 % at 615 cal yrs BP and subsequently resurges to a peak of 32 % at 175 cal yrs BP. *Cliffortia* 2 proliferates from 6 % at 1170 to a peak of 16 % by 505 cal yrs BP, then gradually declines in abundance to 9 % at the top of the cluster.

Forest taxa in PLB1-2 are slightly more abundant and more dynamic than in the preceding cluster (PLB1-1). Celastraceae increases from 5 % at the base of the cluster to a peak of 8 % by 1170 cal yrs BP. For the remainder of the cluster it is rare, apart from a peak to 5 % at 615 cal yrs BP. *Podocarpus* varies between 1 and 8 %, with peaks at 1390, 1060, and 615 cal yrs BP, and troughs at 1500, 1170, 835, 505 and 175 cal yrs BP. Similarly, *Canthium* fluctuates in abundance between 0-8 %, with high values around 1500, 1200, and 395-175 cal yrs BP, and low values at 1390, 1060 and 615 cal yrs BP. *Rhus* is generally of low, homogenous abundance, but peaks to 4 % at 505 cal yrs BP. *Brachylaena* and *Myrica* are less abundant than in the preceding cluster, being present in relatively low abundances in PLB1-2.

The proportion of damaged pollen, although erratic, generally decreases from a maximum of 29 % at 2730 cal yrs BP towards the base of PLB1-1, to close to zero by the top of cluster PLB1-2. The proportion of concealed pollen does not manifest any prominent trend, though is generally higher in cluster PLB1-2 than in PLB1-1.

5.1.5. Platbos 1 Fossil Charcoal

Samples at 250, 130 and 60 cal yrs BP differ significantly from the majority of samples and have notably higher influx rates for both charcoal classes (Figure 5.6). The sample at 130 cal yrs BP has particularly high rates of influx, and corresponds to an historical date of c. AD 1820. Removal of the most extreme of these samples (at 130 cal yrs BP) from the data enhances resolution on trends in the charcoal stratigraphy through the preceding record.

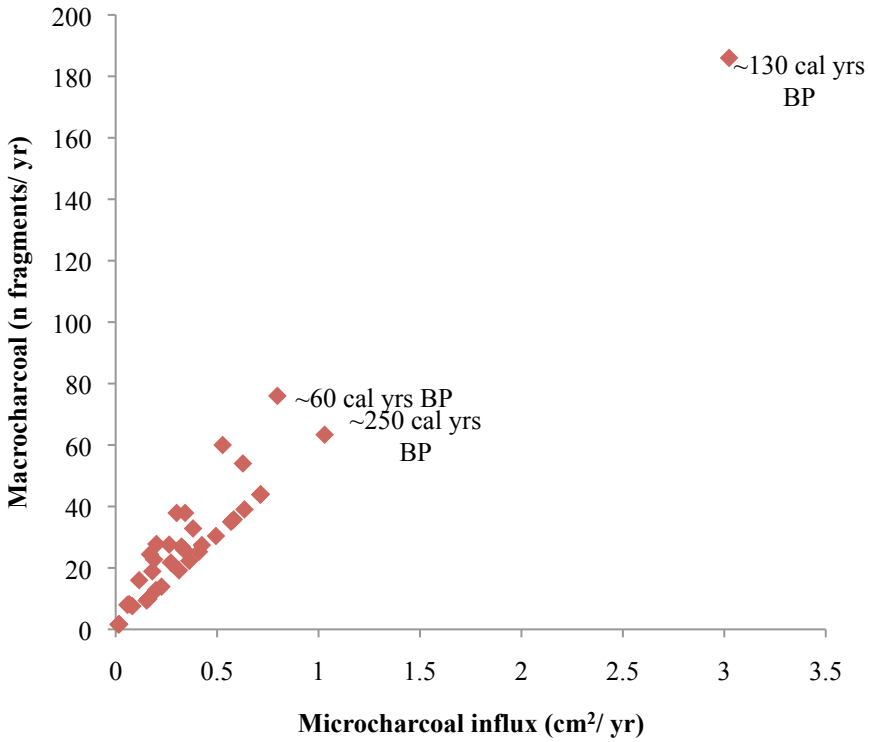

Figure 5.6. Scatter plot of Platbos 1 macro- and microcharcoal accumulation rate data with outliers indicated.

Trends in the micro- and macrocharcoal data are remarkably similar (Figure 5.7). The lowermost sample for which an influx rate was calculable was at 2890 cal yrs BP. It records a rate of 0.6 $cm^2/ cm^3/ yr^{-1}$, which is the highest recorded in cluster PLB1-1. Very low values (<0.1) are then recorded until 2355 cal yrs BP, whereupon influx rates fluctuate between 0.2 and 0.4 $cm^2/ cm^3/ yr^{-1}$ for the rest of the cluster. Rates remain similar in PLB1-2 until 835 cal yrs BP, where after an increase to 0.7 $cm^2/ cm^3/ yr^{-1}$ at 615 cal yrs BP is recorded. Subsequently, prominent peaks emerge in the

data to 1.0 cm^2/ cm^3/ yr^{-1} at 285 cal yrs BP (c. AD 1675) and 3.0 cm^2/ cm^3/ yr^{-1} at 130 cal yrs BP (c. AD 1820). The macrocharcoal data closely mirrors the microcharcoal data. Influx rates in cluster PLB1-1 range between 1.5 and 38 fragments/ year, the highest rates being between 2140 and 1860 cal yrs BP. In cluster PLB1-2, peaks of 44, 63 and 186 fragments/ year occur at 615, 285 and 130 cal yrs BP, respectively.

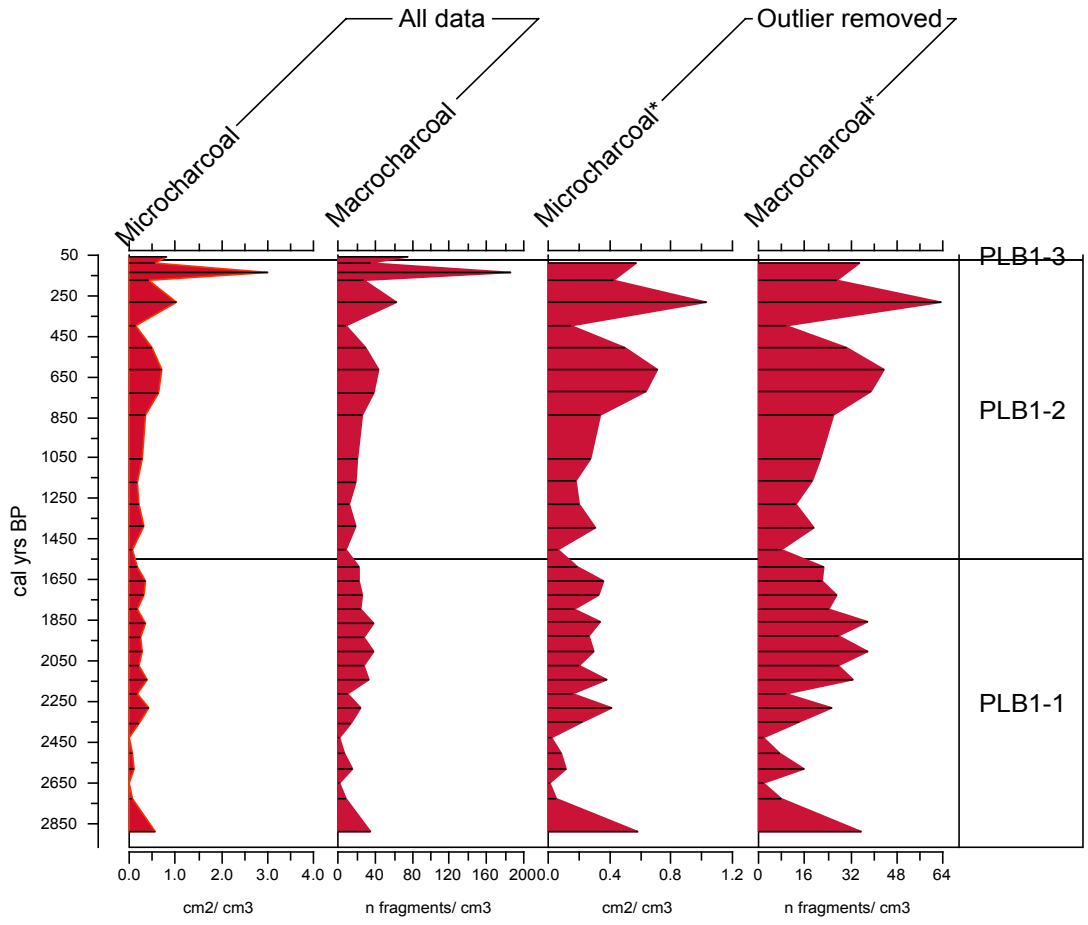

Figure 5.7. Platbos 1 fossil charcoal data. Microcharcoal is expressed as $cm^2/cm^3/yr$, and macrocharcoal as the number of fragments/ yr. Data with outlier at 130 cal yrs BP excluded is also presented (right). Clusters based on the total land-pollen data are indicated on the right.

5.1.7. Platbos 1 Non-Land Pollen and Non-Pollen Palynomorphs

Non-land pollen and non-pollen palynomorph types are presented in Figure 5.8. Cyperaceae accumulated rapidly between 2890 and 2140 cal yrs BP, with highs of 800-2300, 3800, 4600 and 1600 grains/ $year^{-1}$ at 2890-2655, 2505, 2355 and 2140 cal yrs BP, respectively. For the remainder of PLB1-1 and PLB1-2, rates generally fluctuate between 100 and 1500 grains/ $year^{-1}$, with higher values centred on 1725,

1390, 1055, 725 and 285 cal yrs BP. *Gunnera* is present only in the lower portion of PLB1-1 between 2890 and 2140 cal yrs BP and is rare relative to Cyperaceae with influx rates varying between 0 and 210 grains/ year^{-1}. The trends in *Myriophyllum* influx to some extent oppose those of Cyperaceae and *Gunnera*, being generally lower in PLB1-1 than in PLB1-2. Slight peaks in the lower cluster occur at 2890, 2655, 2140, 1725-1655 cal yrs BP, and are of orders <450 grains/ year^{-1}. In cluster PLB1-2 progressive peaks in influx to 490 and 1550 grains/ year^{-1} occur at 285 and 130 cal yrs BP.

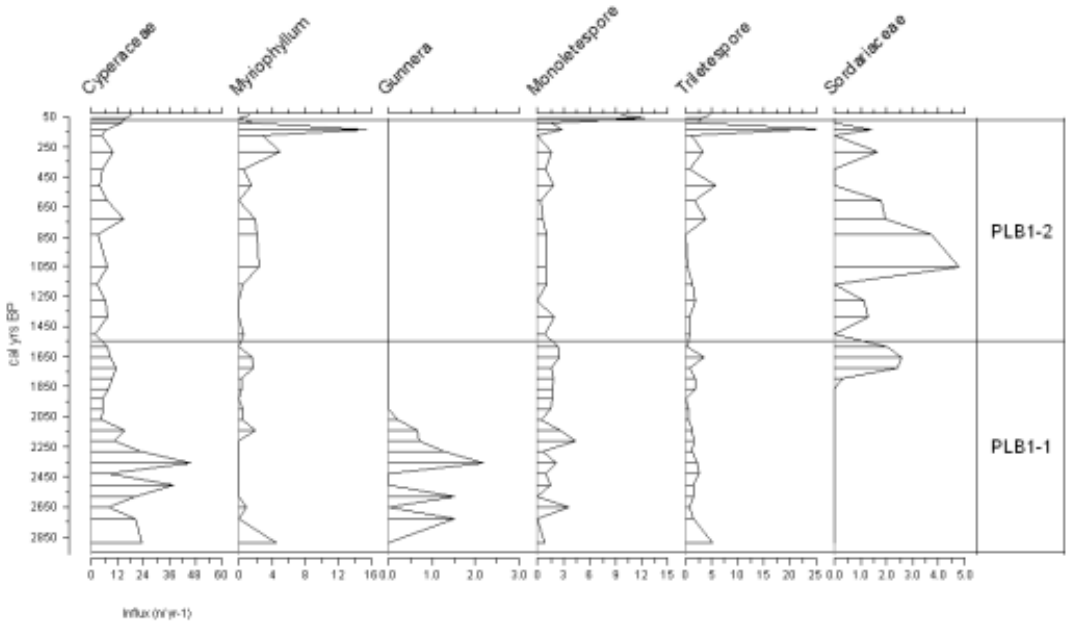

Figure 5.8. Stratigraphic plot of non-land pollen and spores from Platbos 1. Pollen data are presented as n/ cm^3/ yr, and spore data are presented as number of spores/ yr x 10^{-2}.

The concentration of monolete spores is highly erratic in clusters PLB1-1 and PLB1-2, ranging between 0 and 430 spores/ year^{-1}, with no discernible trends (Figure 5.8). Trilete spores are generally more abundant, are less erratic and exhibit identifiable trends. The highest influx rate in cluster PLB1-1 is 530 spores/ year^{-1} at 2890 cal yrs BP. Thereafter rates vary between 0 and 360 spores/ year^{-1}, and remain similar in the lower portion of PLB1-2. An increase in this rate then occurs in the upper portion of PLB1-2, with peaks to 390, 580, 330 and 2680 spores/ year^{-1} at 725, 505, 285 and 130 cal yrs BP, respectively.

Spores of coprophilous fungi Sordariaceae exhibit a clear trend. From the base of the record at 2890 until 1725 cal yrs BP, spores of this type are absent. Subsequently, and prior to the onset of cluster PLB1-2, the influx rate peaks to 260 spores/ year^{-1} at 1590 cal yrs BP. Through cluster PLB1-2 influx rates vary considerably, the highest being 110-130 spores/ year^{-1} between 1280 and 1170 cal yrs BP, 480-180 spores/ year^{-1} from 835 to 505 cal yrs BP, and 170 spores/ year^{-1} at 285 cal yrs BP.

5.1.8. Platbos 1 Non-Metric Multidimensional Scaling

The scree plot generated for Platbos 1 (Figure 5.9) indicated a two-dimensional solution with a stress value of 15 which is an adequate performance. Although addition of a third, fourth, fifth and sixth dimension improves the stress value, the resulting ordinations added little insight as they did not differ greatly from the second or third dimensions.

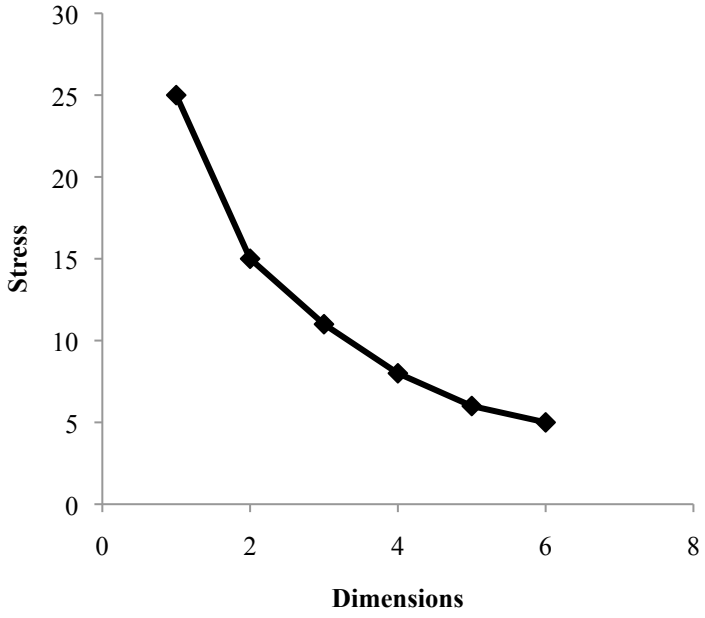

Figure 5.9. Scree plot indicating the number of NMDS dimensions associated with stress.

Two major groups that emerge from a bi-plot of the first and second dimensions (NMDS1 and NMDS2, respectively) are clear (Figure 5.10). The first is situated on the right of the plot, the second on the left, and these correspond to clusters PLB1-1 and PLB1-2. Group 1 includes samples dating from 2969 until 1725 cal yrs BP, which

are distributed within the range of 0.5 to 0.0 along NMDS1. Taxa associated with these samples are *Brachylaena*, Celastraceae, Restionaceae, *Berzelia*-type and *Cliffortia* 1. As time progresses in Group 1, samples move in a positive direction along NMDS2, younger samples being more associated with Lamiaceae and Poaceae than those previously mentioned.

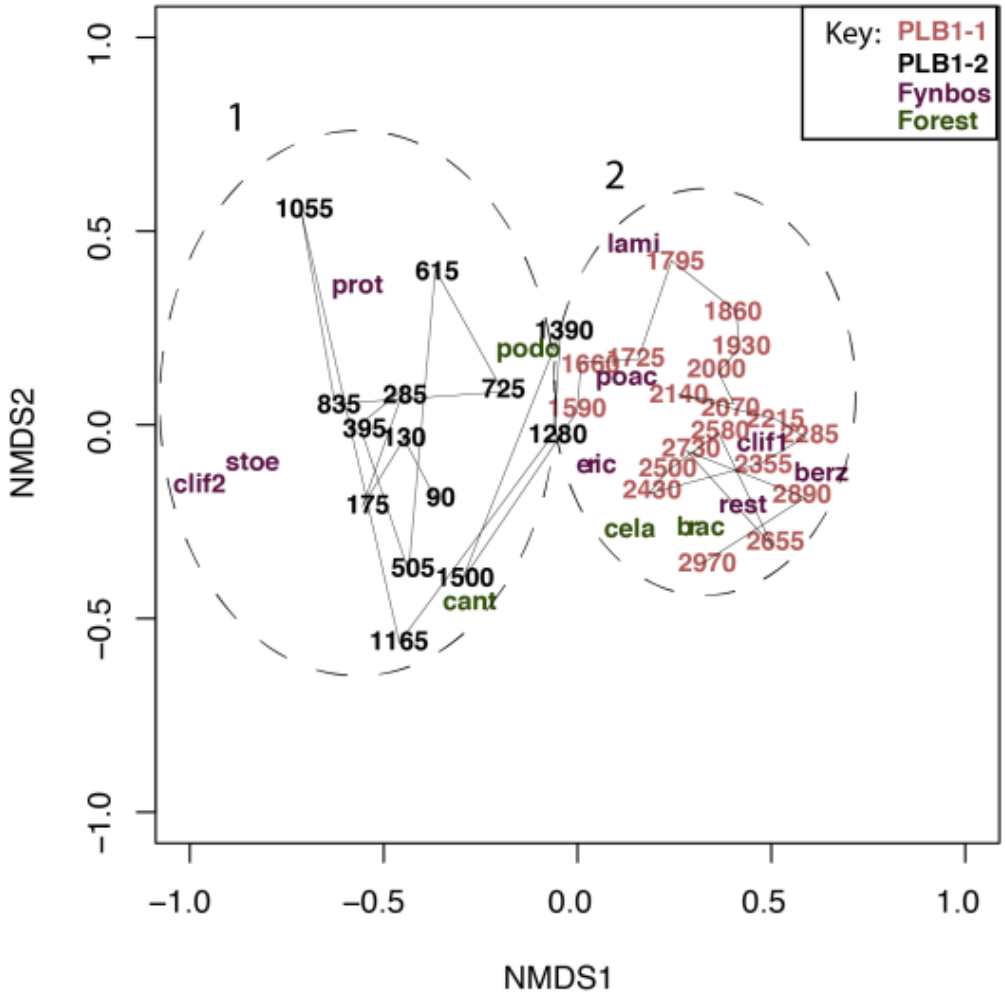

Figure 5.10. NMDS ordinations for Platbos 1. The nature of change through time is indicated by the solid line, which connects temporally sequential samples. Major groups are identified and indicated by dashed lines. Prot = Proteaceae, stoe = Stoebe-type, clif2 = Cliffortia 2, cant = Canthium, podo = Podocarpus, eric = Ericaceae, poac = Poaceae, cela = Celastraceae, brac = Brachylaena, rest = Restionaceae, clif1 = Cliffortia 1, berz = Berzelia, lami = Lamiaceae. Taxa labels are coloured according to biome affinity, and samples are coloured according to clusters identified in the dendogram.

The transition from Group 1 to Group 2 occurs between 1725 and 1655 cal yrs BP. Taxa characteristic of this second group are *Podocarpus, Canthium*, Proteaceae and, to the greatest extent, *Cliffortia* 2 and *Stoebe*-type. Samples are weakly organized along NMDS2 in the second grouping, with no strong direction of change through time.

5.2. DISCUSSION 1: BETWEEN-BIOME RESISTANCE AT PLATBOS 1

At the between-biome scale, fynbos appears highly resistant to environmental change over the past 3,000 years at Platbos 1. Only minor fluctuations in the abundance of the forest and fynbos biomes occurred over the study period. This is despite evidence of substantial environmental variability in proxies for local hydrology, fire and herbivory (Figures 5.11, 5.12), as well as in regional palaeoclimatic records (Bateman, et al. 2011; Chase and Meadows, 2007; Carr, et al. 2006; Chase, et al. 2013; Kirsten, 2014; Martin, 1968; Talma and Vogel 1992). Reasons for this between-biome stability are highlighted and discussed in the following section with reference to changes in clusters PLB1-1 and PLB1-2 (2975-1545 cal yrs BP and 1545-50 cal yrs BP, respectively).

5.2.1. Resistance to Changes in Climate and Fire in a Warming Climate (2975-1545 cal yrs BP)

In the south western Cape, where true Mediterranean-type climate dominates at present, afrotemperate forests are mostly restricted to moist valleys as the prevalent summer aridity causes drought-induced stress and mortality (Manders, 1990, 1992; Coetsee, et al. 2015). In addition, fire inhibits the expansion of forest into open fynbos areas. Therefore, we may expect forest expansion in times of cooler and/ or wetter climate, and/ or when fire is less prevalent, and fynbos expansion in times of drier/ hotter climate, associated with more frequent fire. Fire regimes are also modified by vegetation type, however, and the climate-fire-vegetation relationship is complex. It is feedback processes at this nexus which here best explains the resistance of the fynbos-forest boundary at Platbos.

From 4000-2000 cal yrs BP, the 'neoglacial', Platbos would have experienced temperatures some 1^{o}C cooler than present (Jerardino, 1993, 1995). (Talma and Vogel, 1992) (Figure 5.11). Holocene cooling in the southern Cape is generally associated with increased influence of the winter rainfall westerlies system and disruption to easterly moisture bearing systems in summer, which results in an increased rainfall amount but also increased summer drought (Bateman, et al. 2011; Carr, et al. 2006; Chase, et al. 2013; Kirsten, 2014). At Platbos 1, the phase between around 2,975 and 2,250 cal yrs BP is associated with high influx rates of Cyperaceae, *Gunnera perpensa* and, to a lesser extent, *Myriophyllum spicatum* and fern spores (Figure 5.11). The wetlands at Platbos are perennially fed by drainage of the Tsitsikama Mountains (Vlok, et al 2008), and therefore expand in response to increased total annual precipitation. The high influx rates of these wetland taxa are therefore interpreted as indicating enhanced influence of the winter rainfall zone and dominance of a winter-wet/ summer dry Mediterranean-type climate during the period encompassing these extremely low charcoal influx rates.

At Platbos 1, the prevalence of highly seasonal conditions associated with low temperatures of the neoglacial would have inhibited burning through drought-induced limitation of biomass production (i.e. fuel) (Steenkamp, et al. 2008). This corresponds with the lowest recorded charcoal values at Platbos 1 which occur between 2,650 and 2450 cal yrs BP, within the lower samples of cluster PLB1-1. This decrease in fire frequency could potentially allow forest expansion (Kraaij, et al. 2014; Slingsby, et al. 2014), but the pollen record shows that this did not occur. Instead, the results suggest that the growth of forest species in open fynbos habitat was likely restricted by summer-drought induced growth limitation and/ or mortality (Coetsee, et al. 2015). This suggests that the fynbos state was resistant to invasion by forest under a cooler climatic scenario than present. Given future environmental change scenarios for increased temperatures (Engelbrecht, et al. 2009; Hewiston and Crane, 2006; Tadross, et al. 2005), the ecological factors promoting and maintaining resistance during past warm events might be more useful to examine.

At the end of the neoglacial, prevalent cool conditions were interrupted by significant warming. In the southern Cape this is recorded in the Cango Caves speleothem record

as a temperature increase of approximately -1°C to +1.5°C relative to present averages between around 2,400 and 2,000 cal yrs BP (Talma and Vogel, 1992). Regionally, this temperature increase is linked to a shift from Mediterranean-type climate (as outlined above), to one with lower total rainfall but also less pronounced summer drought under increased influence of the subtropical easterlies (Bateman, et al. 2011; Carr, et al. 2006; Chase, et al. 2013; Kirsten, 2014; Martin, 1968; Talma and Vogel 1992). At Platbos 1, after 2250 cal yrs BP the wetland indicators become substantially less abundant and their reduced influx over the period is interpreted as indicating wetland recession as a result of a reduced influence of the westerlies. The increased influence of the subtropical easterlies, however, would have reduced summer aridity stress which in turn might have facilitated the rapid establishment of forest pioneers in fynbos habitat (Coetsee, et al. 2015; Hoffmann, et al. 2012). However, under increased influence of summer advective systems, biomass production (Steenkamp, et al. 2008) and fire frequency are likely to have increased (Kraaij, et al. 2014). This would have reduced the time in which pioneers have to establish and develop fire resistant properties, or attain the 'fire resistance' threshold (Hoffmann, et al. 2012). Increasing charcoal influx at Platbos 1 through cluster PLB1-1, particularly from 2,400 to around 1,800 cal yrs BP, supports this interpretation.

The resistance of fynbos to invasion by forest at Platbos can therefore be viewed as resulting from negative feedbacks involving a complex interplay between the southern African winter/ summer rainfall systems under cooler/ warmer conditions (Chase, et al. 2013) and (1) the availability of moisture and nutrients for biomass production and the effect this has on the length of the fire-free interval and (2) the physiological characteristics of forest pioneers that determine growth rates and time to fire resistance (Coetsee, et al. 2015; Keeley, et al. 2012; also see Hoffmann, et al. 2012). In theoretical terms, negative feedbacks in the bi-stable system emerge from interactions between extrinsic abiotic forcing, intrinsic abiotic-biotic interactions, and disturbance (Williams, et al. 2011). These relationships maintained a stable ratio between the potential energy of the state to move in the basin of attraction (Holling, et al. 2002; Scheffer, et al. 2001) and the relative proximity of the transition threshold (Briske, et al. 2008), resulting in a highly resistant biome boundary (Hodgson, et al. 2015). Thus, the data show that the fynbos forest boundary is resistant to both increases and decreases in temperature, due to the alternate effects of fire and drought

on the forest ecosystem.

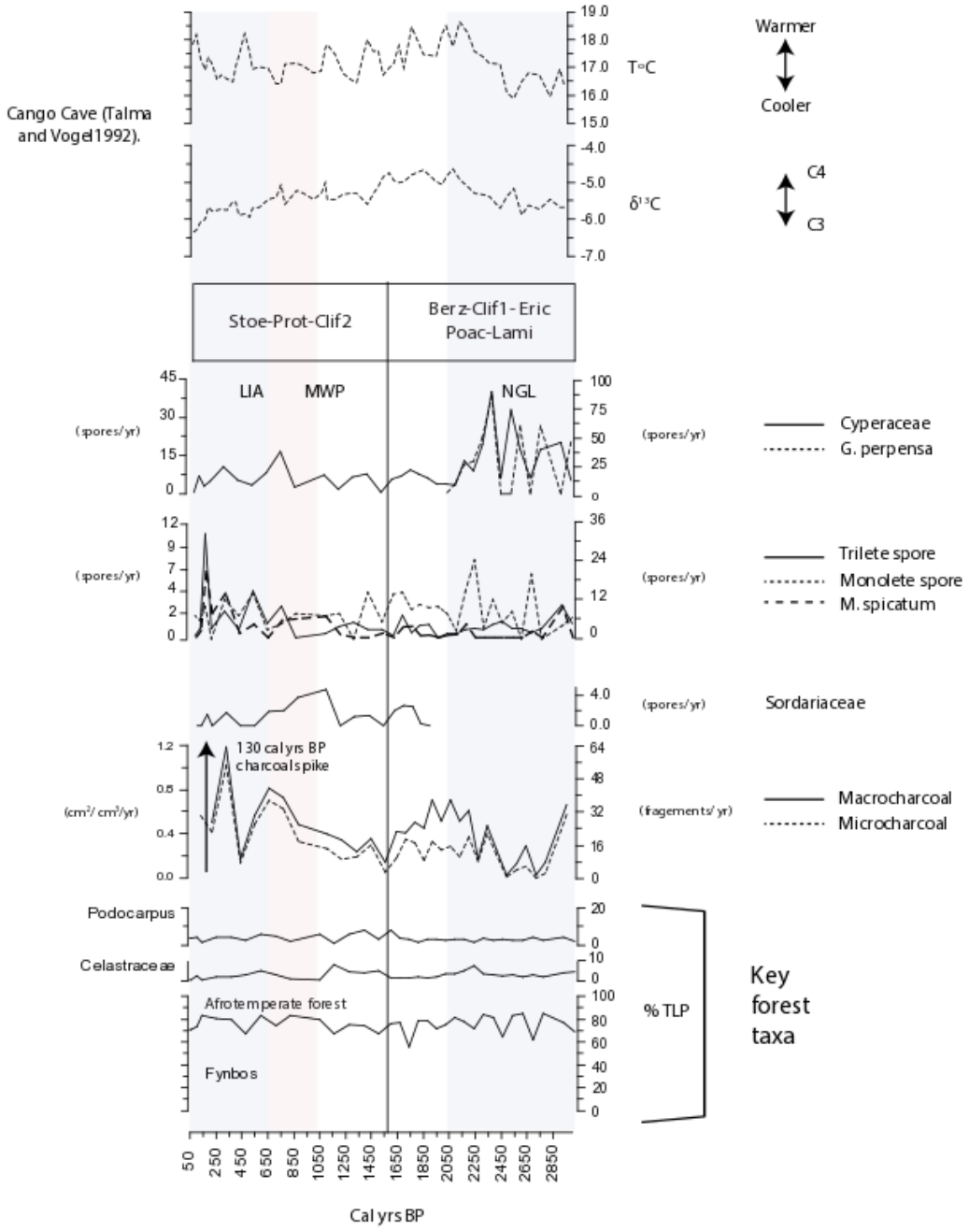

Figure 5.11. Platbos 1 between-biome palaeoecological summary. The bar overlying the Platbos 1 proxies indicates dominant fynbos assemblages for statistically significant portions of the record. Stoe = Stoebe-type; Prot = Proteaceae; Clif2 = Cliffortia 2; Berz = Berzelia-type; Clif1 = Cliffortia 1; Eric = Ericaceae; Poac = Poaceae; Lami = Lamiaceae. Above this are the stable carbon isotope and temperature reconstructions from Cango Cave (Talma and Vogel, 1992). LIA = Little Ice Age (LIA; 650-50 cal yrs BP/ AD 1,300-1,800); MCA = Medieval Climate Anomaly (1050-650 cal yrs BP/ AD 900-1,300); NGL = Neoglacial (4,000-2000 cal yrs BP).

5.2.2. Changes in the Climate-Biomass-Fire Relationship During PLB1-2 and their Expression in the Charcoal Record (1545 to 50 cal yrs BP)

The latter phase of the record spans 1545 to 50 cal yrs BP. During this time, the fynbos-forest boundary remained as stable as it was during the previous phase (PLB1-1; 2975-1545 cal yrs BP). From around 1050 cal yrs BP at Platbos, charcoal influx increases substantially and continues to do so until 650 cal yrs BP, where after influx declines rapidly (Figure 5.11). Perhaps as might be expected, the highest of these rates are concur with the Medieval Climate Anomaly (MCA; 1050-650 cal yrs BP/ AD 900-1,300), and the rapid decline conforms to the Little Ice Age (LIA; 650-50 BP/ AD 1,300-1,800). Under warmer climatic conditions than present, enhanced easterly flow in fynbos would have promoted production of combustible biomass, inhibiting colonisation of fynbos by forest. This accords well with interpretations of the climate-biomass-fire relationship made earlier and which are related to PLB1-1.

By far the highest charcoal influx rates in the whole of the Platbos 1 record occur between 650 and 50 cal yrs BP. The LIA is well resolved in the palaeohydrological record at Elandsvlei (Kirsten, 2014), where high fluvial discharge is linked to increased total rainfall amount and an intensified temperate westerly system (also see Chase and Meadows, 2007; Chase, et al. 2013; Nicolson, et al. 2013; Weldeab, et al. 2015). Where both fire and summer aridity dominated the system, fynbos would have been particularly impenetrable to forest, and this explains the continued resistance to forest expansion during the period of cooler climate. It is perplexing however that higher charcoal influx rates are associated with relatively cool conditions, which contrasts with the observed relationship during PLB1-1 during the neoglacial.

As is discussed in the following section, PLB1-1 was characterised by fynbos of strongly differing structure, function and composition compared to during PLB1-2. Specifically, the latter type possessed the ability to maintain high biomass growth and fire despite strong summer aridity, therefore explaining the higher charcoal influx rates.

5.3. DISCUSSION 2: WITHIN-BIOME STATE TRANSITION AND RESILIENCE OF FYNBOS AT PLATBOS 1

Despite the resistance of the fynbos biome to the changes in climate and fire regimes described above, there have been significant changes in plant community composition within the fynbos biome itself over the period investigated. The record shows the development of grassy fynbos in response to a climatic warming gradient at the end of the neoglacial between around 2,400 and 2,000 cal yrs BP. The climate remained warm until around 1,850 cal yrs BP. Subsequently, a distinct transition occurs at 1,545 BP, from herbaceous-grassy fynbos to woody-proteoid fynbos. Numerous factors including climate, fire and herbivory can be invoked to explain this shift in vegetation structure, composition and species dominance. Once established, each of these different states in fynbos composition appears to be resistant to change. Hydrological indicator palynomorphs, charcoal, coprophilous fungal spore data from Platbos 1, as well existing palaeoenvironmental records, suggest that extrinsic pressures of climate and livestock herding interacted with internal ecosystem properties such as vegetation flammability and structure to create and maintain differing ecological regimes within fynbos, and combined to force unidirectional changes between ecological regimes. This internal turnover of fynbos taxa may in part explain the apparent resilience of the biome: the biome persists as a distinct entity despite significant changes in the dominance of taxa.

5.3.1. The Development of Grassy Fynbos in a Warming Climate (2,970-1,545 cal yrs BP)

As has been discussed above (see section 5.2.1) PLB1-1 (2975-1545 cal yrs BP) is associated with the end of the neoglacial climatic phase (Jerardino, 1995). During this period, between 2,400 and 2,000 cal yrs BP, temperatures gradually eased from approximately -1^{o}C to +1.5^{o}C relative to present averages (Talma and Vogel, 1992). This increase in temperature has been linked to a shifting of the climatic system toward the summer relative to winter rainfall system (Bateman, et al. 2011; Carr, et al. 2006; Chase, et al. 2013; Kirsten, 2014; Martin, 1968), with a lower annual rainfall amount and wetland recession (see section 5.2.1, Figure 5.12).

Associated with this climatic warming were an increase in biomass production and an increase in fire frequency. The pollen record suggests that this favoured increases in herbaceous-grassy fynbos, which further promoted frequent fire and inhibited survival of woody shrub seedlings. The earliest part of the PLB1-1 cluster (~2,975-2,400 cal yrs BP) is characterised by dominant but declining abundances of *Berzelia*-type and *Cliffortia* pollen (Figure 5.3.1). *Berzelia* are strongly associated with moist soils, seeps and riparian areas (Hugo, et al. 2012; Goldblatt and Manning, 2000; Prins, et al. 2004) (Baard, et al. 2013). *Berzelia*-type co-varies closely with Cyperaceae, supporting a link between winter-rainfall and *Berzelia* abundance. Though conditions likely remained mesic at the site, the local hydrological environment likely shifted from minerotrophic (i.e. fed by within-catchment transfers) to ombrotrophic (i.e. rain-fed) (Charman, 2002).

Across this climatic gradient, from around 2,400 to 1,800 cal yrs BP, abundances of Ericaceae, Poaceae, and Lamiaceae increase, which is indicative of a taxonomic assemblage similar to the present Eastern Grassy Fynbos (Vlok, 2008). This fynbos type is characterised by high fire frequencies due to vigorous biomass production facilitated by equitable climate, high fuel connectivity, and high regional incidence of lightning for ignition (Kraaij, 2014). Increased influx of charcoal at Platbos 1 from around 2,400 to 1,800 cal yrs BP reflects this type of fire regime (Figure 5.12). Ericaceae is the dominant fynbos element in zone PLB1-1, and increases along with Poaceae (Figure 5.12). Ericaceae species, particularly those that characterise the eastern GCFR at present (Ojeda, 1998), tend to be re-sprouters and are adapted to high fire frequencies. They are a consistent component of Eastern Grassy Fynbos (Vlok, 2008), and have been known to invade grasslands (which have very high fire frequencies) where fire frequencies are lowered (Keeley, et al. 2012).

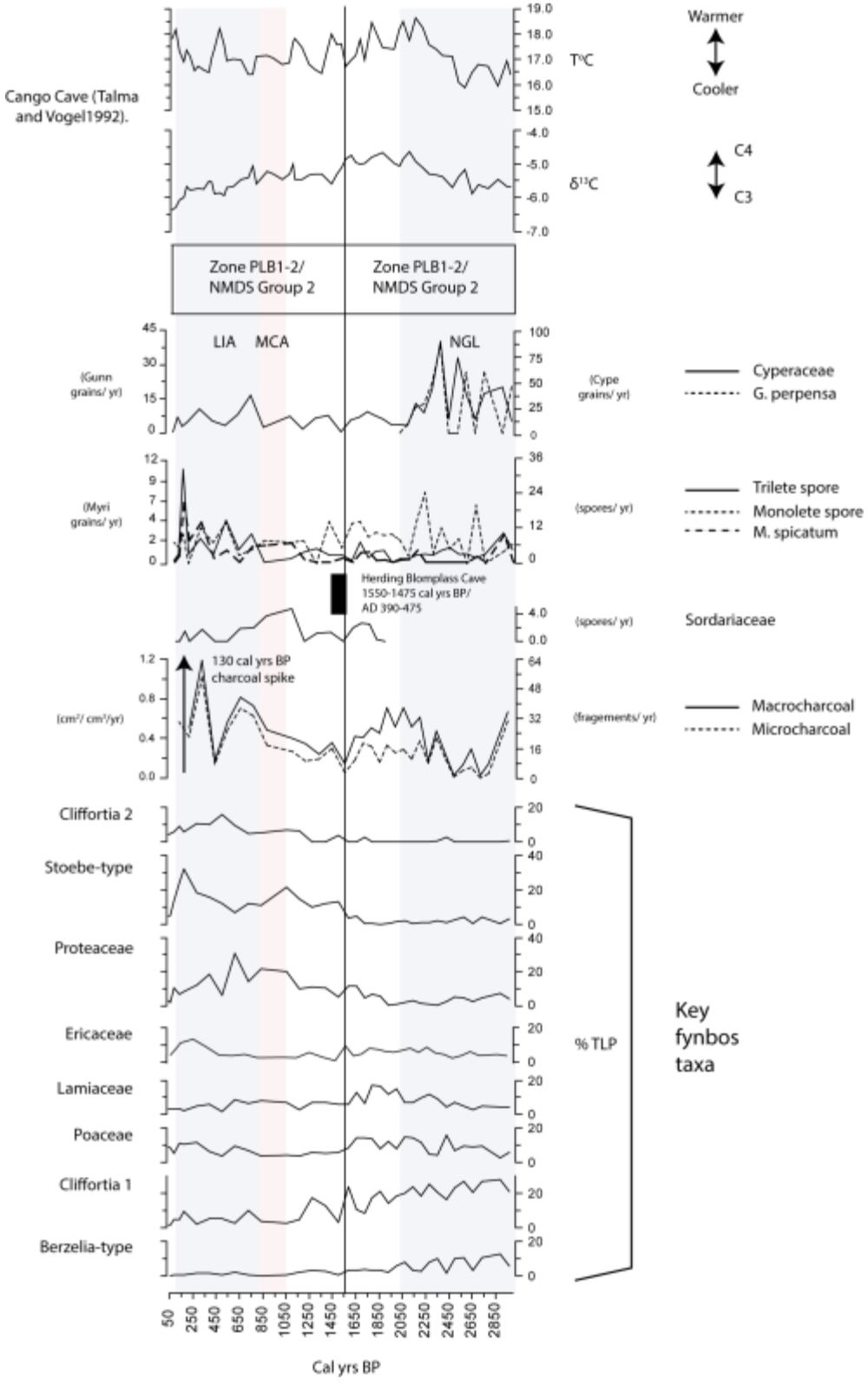

Figure 5.12. Platbos 1 within-biome fynbos palaeoecological summary. LIA = Little Ice Age (LIA; 650-50 cal yrs BP/ AD 1,300-1,800); MCA = Medieval Climate Anomaly (1050-650 cal yrs BP/ AD 900-1,300); NGL = Neoglacial (4,000-2000 cal yrs BP).

Frequent fire promotes the growth of grasses which have short regeneration phases, and suppresses those with longer regeneration phases as well as fynbos woody shrubs (e.g. *Berzelia* and *Cliffortia*) (Keeley, et al. 2012). Further, the proportion of grass in fynbos communities can increase following fire as grasses rapidly utilise released nutrients (Ballantyne, 2010; Hoffman, et al. 1987; Kruger, 1977, 1987), which can create a feedback loop in favour of grassiness.

In particular, summer rainfall promotes the proliferation of C_4 grasses that have higher photosynthetic and respiratory efficiencies than do C_3 fynbos shrubs (Vogel, et al. 1978), resulting in further enhanced biomass accumulation and frequent fire. At Cango Caves, stalagmite $\delta^{13}C$ composition indicated C_4 biomass production began to increase from around 2,650 cal yrs BP then stabilised from around 2,150 to 1,550 cal yr BP (Figure 5.2.1). Talma and Vogel (1992) calculated that at that time C_4 photosynthetic production accounted for approximately 50 % of total primary productivity. This suggests firstly that the observed increase in grass at Platbos 1 likely reflects a broader, landscape-level change, and secondly that this change was of substantial magnitude.

High fire frequency similarly favours herbaceous forbs (Linder and Ellis, 1990) such as those within the Lamiaceae (Figure 5.12) (e.g. *Leonotis, Stachys* and *Plectranthus*) (Gendenhuys, 1993). Rapid formation of a dense, herbaceous vegetation layer in grassy fynbos restricts recruitment of woody shrubs, and further promotes biomass accumulation, flammability, high fire frequency and perpetuates the open, herbaceous-grassy fynbos state. The development of the state, although initiated by abiotic forcing (climate), is also strongly influenced by intrinsic biotic processes involving fire and vegetation.

5.3.2. The Grassy to Proteoid Fynbos Transition (1545 cal yrs BP): Interacting Roles of Climate, Fire and Land-use Change

The transition to zone PLB1-2 at 1545 BP, is marked by a transition from grassy to proteoid fynbos. The transition is characterised by decreased abundance of the herbaceous taxa within the Poaceae and Lamiaceae, a decrease in *Cliffortia* 1 and *Berzelia*, and lowered charcoal influx until around 1250 cal yrs BP. The post-transition vegetation is dominated by taller, woody fynbos shrubs of Proteaceae,

Stoebe-type and *Cliffortia* 2 (Figure 5.12). The environmental and ecological scenario surrounding this shift is complex. While interactions between vegetation and fire are clear, the roles of climate and land-use change in driving these changes is more difficult to ascertain.

The first major floristic change preceding the shift to proteoid fynbos appears to be an increase in the abundance of Proteaceae from around 1,800 cal yrs BP. Kraaij et al. (2013d) determined that fire return periods above a threshold of > 9 years would be required to allow development and persistence of Proteaceae populations in the grass-rich east coast fynbos of the Tsitsikama and Outeniqua Mountains. Fire exclusion experiments have shown that sclerophyllous fynbos vegetation invades grasslands at the eastern limits of the fynbos biome where the fire-free interval exceeds ten years or more (Keeley, et al. 2012). Reduced macrocharcoal influx from around 2000-1800 cal yrs BP therefore likely reflects reduced fire frequency. A reduction in fire frequency from that associated with grassy fynbos, which developed through zone PLB1-1, would have been required to allow reproduction of an initial pioneer parent plant and subsequent proliferation of the taxon.

Reduced fire-frequency and the establishment of the Proteaceae population might be attributable to decreased primary production associated with climatic cooling and increased seasonal aridity under dominance of the winter-rainfall zone (Chase and Meadows, 2007; Chase, et al. 2013). Regionally cooler temperature between around 1750 and 1250 cal yrs BP are evident at Cango Caves (Talma and Vogel, 1992). Accordingly, the palaeohydrological record at Elandsvlei records the highest freshwater inflow in the late Holocene between around 1,650 and 1,150 cal yrs BP, apparently reflecting strong influence of the winter-rainfall zone (Kirsten, 2014). Similarly, depleted $\delta^{13}C$ values at both Cango Caves (Talma and Vogel, 1992) and Seweweekspoort (Chase et al. 2013) likely reflect increased rainfall seasonality (Vogel, et al. 1978) and/ or decreased plant water-use efficiency under summer drought (Chase, et al. 2013; Chase, et al. 2012). Despite the consistency of regional records indicating climatic changes at this time, little substantial change is seen in the hydrological indicators at Platbos 1 during this period (Figure 5.12). Nevertheless, reduced charcoal production at Platbos 1 is indicative of reduced primary production under drought limitation, and additional indications of the local palaeohydrological

conditions can be gleaned from the pollen record and associated vegetation functional types.

Members of the Proteaceae family employ isohydric hydraulic strategies that regulate stomatal and xylem conductivity, and so promote resistance to drought-induced mortality (Skelton, et al. 2015; West, et al. 2012). Proteaceae seeds have also been indicated as very tolerant of desiccation under drought conditions (Arnolds, et al. 2015). Further, members of the family possess deep rooting systems that allow access to water reserves at lower levels of the soil profile during drought. They are therefore well adapted to Mediterranean-type climate with pronounced summer aridity. *Stoebe*-type likely represents a similar ecohydrological functional type (discussed further below). In contrast, grasses and herbs of Lamiaceae are shallow-rooted compared to shrubs in the southern Cape making them vulnerable to summer drought, and C_4 grasses are particularly vulnerable to summer drought (Talma and Vogel, 1978). A drought-resistant *versus* drought-sensitive functional type classification therefore suggests that a change in the hydrological environment did occur at Platbos 1, and that the drier conditions favoured the shift to proteoid fynbos. The shift in the dominance of the westerlies and easterlies would have reduced fire frequency as a result of decreased lightning-induced fires (Kraaij, et al. 2013a,b,c) allowing slower maturing Proteaceae to establish and shade out grasses (Cowling and Potts, 2015).

Reduced fire during this time period might also reflect reduced biomass availability due to consumption by large herbivores (see Bond and Keeley, 2005). At around 1,800 cal yrs BP the influx of Sordariaceae spores increases, suggesting increased abundance of large herbivores occurred at the same time as the decrease in fire. This is also contemporaneous with the earliest archaeological evidence of herding in the southern Cape comes from Bloomplaas Cave in the Still Baai area and is dated to around AD 390-475 (1550-1475 cal yrs BP) (Damm and Hagedorn, 2010; Deacon, 1995), which lends support to the interpretation that the increased Sordariaceae influx reflects introduced livestock (likely sheep and goats; Deacon, 1995). Herbivores consume biomass, in particular plants that commonly fuel fire such as grasses (Bond and Keeley, 2005), and may have reduced biomass available for fuel as well as fuel connectivity.

The change at 1545 cal yrs BP represents the major first order shift in the record, and zones PLB1-1 and PLB1-2 represent alternative stable states (Holling, 1973; Lewontin 1969; Scheffer, et al. 2001; Scheffer, et al. 2001). Abrupt shifts of this type have been linked to interactions between divers of change that combine to force a shift of disproportionate magnitude (Beisner, et al. 2008). Indeed, the wider literature suggests that that a combination of drivers are required to induce transitions between alternative stable states (Willis, et al., 2010). Here, it appears that both climate and land-use change substantially altered the fire regime, which resulted in a state shift.

5.3.3. Resistance of the Proteoid State to Grassy Fynbos Recovery: Biotic Inhibition of Hysteresis post-1545 cal yrs BP

From 1545 cal yrs BP until clearance of Platbos for pine plantation, the proteoid fynbos state remains dominant. This is despite climatic conditions associated with the Medieval Climate Anomaly (MCA; 1050-650 cal yrs PB/ AD 900-1,300) that may have been similar to those expressed following the end of the neoglacial between 2250 and 1850 cal yrs BP when grassy fynbos developed. Proteaceae, *Stoeb*e-type and the unspecified taxon *Cliffortia* 2 characterise the pollen spectra, and influx rates of both charcoal and wetland indicator taxa increase in broad concert from around 1250 cal yrs BP. These patterns do not conform clearly to the regional palaeoenvironmental record and, it is argued here, this represents strong biotic control on ecosystem structure and function.

The timing and magnitude of the MCA and its impacts is regionally and globally variable, and the MCA is not shown clearly in the southern Cape palaeotemperature record (see Chase, et al. 2013; Nicholson, et al. 2013; Talma and Vogel, 1992; Tyson and Lindesay, 1992; Tyson, et al. 2000). Further, there is no clear expression of the event in the palaeohydrological record at Platbos 1, nor is it well represented in moisture indicators at Cango Caves (Talma and Vogel, 1992) and Seweweekspoort (Chase, et al. 2013). However, a clear and marked decrease in freshwater input occurs at Elandsvlei between 1150 and 825 cal yrs BP, and is indicative of weakened temperate westerlies, strengthened tropical easterly flow, and reduced rainfall seasonality (Kirsten, 2014). Freshwater flow into Elandsvlei at this time appears to

have been similar to those following the neoglacial termination at around 2250 to 1850 cal yrs BP, which is interpreted as reflecting a similar palaeoclimatic scenario.

The resistance of proteoid fynbos to a return to climatic conditions previously favouring grassy fynbos therefore suggest that proteoid and grassy fynbos are hysteretic alternative stable states (Beisner, et a. 2003), whereby both may persist under the same environmental parameters. Reversion of a state shift is likely to be inhibited by internal feedback processes that promote resistance to extrinsic forcing. For example, stands of *E. rhinocerotis,* an obligate seeder, is known to reproduce abundantly following fire. Offspring often form dense stands which subsequently suppress establishment of competitors (Keeley, et al. 2012; Proksch, et al. 1982). These stands then become self-sustaining through continued prolific seed production and high intensity burns, which stimulate germination and establishment of the abundant seed bank. Historical observations from the southern Cape Tsitsikama region (Phillips, 1930; Acocks, 1975) suggest that under conditions of increased fire frequency there is a trend towards dominance of asteraceous shrubs such as *Stoebe* spp. and *E. rhinocerotis*. Such shifts have more recently been recognised as resistant alternative stable states that will not revert naturally and so require active management intervention (Curtis 2013; Forbes, 2014; Keeley, et al. 2013; also see 'hysteresis' in Oliver, et al. 2015).

Similarly, Burger and Bond (2015) found particularly high flammability in fire-stimulated recruiting fynbos species of *Leucadendron*, *Protea*, *Elytropappus*, *Stoebe*, *Cliffortia* and common Asteraceae shrubs including *Metalasia* (Figure 5.1.2), all of which are characteristic of PLB1-2. The fire-adapted traits so prevalent among the fynbos flora may contribute to potential alternative stable states within the biome when climatic and land-use parameters combine to force the system in a similar direction.

The high influx of Sordariaceae between around 1100 and 1050 cal yrs BP suggests that the shift toward more equitable climate was associated with increased abundance of large herbivores, possibly associated with Khoi herders (Damm and Hagedorn, 2010; Deacon, 1995). This increase in herbivory may have helped to stabilise the proteoid fynbos and increase its resistance to proliferation of grasses.

In order for grasses and herbs to have proliferated during the MCA at Platbos 1, a perturbation would have been required of sufficient magnitude to override the resistance of woody-proteoid fynbos. The pathway by which this might happen would involve grasses and other herbaceous taxa such as Lamiaceae rapidly generating enough biomass for fire prior to *Stoebe*-type and other slow growing fynbos taxa attaining the 'fire resistance' threshold (Hoffmann, et al. 2012). Even though climatic conditions may have been favourable to growth of grasses and herbs during the MCA, herbivory would have restricted their dominance and hence inhibited significant impact on the woody-proteoid state.

At present, Tsitsikamma Plateau Proteoid Fynbos (Vlok, et al. 2008) can be identified in untransformed areas with similar geographic and topographic setting to Platbos. This fynbos type is dominated by tall (up to 10 m) Proteaceae and *E. rhinocerotis*, and is characterised by low fire frequencies (>20 yrs). By implication of this study, this may not reflect the climatic equilibrium state, but rather a resistant alternative stable state that formed some 1500 years prior in response to the dual pressures of climate and land-use change, their effects on fire and vegetation, and subsequent internal biotic engineering processes.

5.4. SYNTHESIS OF BETWEEN- AND WITHIN-BIOME DYNAMICS AT PLATBOS 1

It is well established that the realised distribution of forest in the southern Cape is dependent on fire refugia associated with abutting mountain ranges of the Cape Fold Belt (Geldenhuys, 1994). In the contemporary biogeographic context, the model provided by Geldenhuys (1994) provides an ample explanation of the distributions of fynbos and forest. However, in the context of shifting climatic and fire regimes (Altweg, et al. 2014; Hoffmann, et al. 2012; Keeley, et al. 2012), the palaeoecological record has demonstrated that a more complex mechanistic understanding is required, which should incorporate shifting climatic parameters - in particular rainfall seasonality and summer drought intensity - through time and associated changes in the relationships between abiotic, biotic and disturbance regimes. In a broader context, this parallels the shift in thinking within ecological theory from community-based concepts (e.g. ball-in-cup model) (Drake 1991; Lewontin 1969; May 1977) to

dynamic ecosystem models (e.g. state-and-transition model) (Beisner et al 2003; Scheffer et al 2001; Vetter 2009). Such a dynamic perspective would not be possible without the temporal dimension afforded by palaeoecological data, which highlights the crucial role of palaeoecology in understanding ecological resilience and alternative stable states over decadal to millennial timescales.

At the within-biome scale, an ecosystem state shift (Holling, 1973; Lewontin 1969; Scheffer, et al. 2001) occurred at around 1545 cal yrs BP. Vegetation re-organised from a low, open grassy-herbaceous fynbos to a taller, woody-proteoid fynbos. The woody-proteoid state was dominated by the invasive indigenous taxon *Stoebe*-type, which likely represents the indigenous invader *Elytropappus rhinocerotis*. As such, the change reflects the widely recognised state shift within the fynbos biome involving transition from a grass-rich state with frequent fire, to a grass-poor state dominated by the unpalatable shrub *Elytropappus rhinocerotis* ('renosterbos') (Rebelo, et al. 2006). The state is known to be highly resistant and maintained through interactions between herbivory and fire, but its historical persistence is not well resolved (Radloff, 2008). This study has revealed the development of the state in response to land-use and fire-regime change associated with introduction of livestock to the area and the spread of Khoi pastoralism over 1,500 years ago (Deacon, 1995; Marean, et al. 2014; Sadr, 2014).

The change at 1545 cal yrs BP represents a major first order shift in the record, and zones PLB1-1 and PLB1-2 represent alternative stable states (Holling, 1973; Lewontin 1969; Scheffer, et al. 2001; Scheffer, et al. 2001). Abrupt shifts of this type have been linked to interactions between divers of change that combine to force a shift of disproportionate magnitude (Beisner, et al. 2008). Indeed, the wider literature suggests that that a combination of drivers is required to induce transitions between alternative stable states (Willis, et al., 2010). Here, it appears that both climate and land-use change substantially altered the fire regime, which resulted in a state shift. The floristic nature of the resulting community was subsequently dependent on interactions between plant functional types, the regional and local climatic regime, and land use.

Intriguingly, the state shift may have been initiated sometime earlier by increased summer aridity and/ or livestock and the proliferation of Proteaceae centuries earlier from around 1850 cal yrs BP. Both these environmental stressors would favour Proteaceae and, in doing so, alter the fire and disturbance regime in favour of conditions suitable for other taxa with similar traits, acting as a 'biotic modifier' or 'ecosystem engineer' (Linder, et al. 2012). Palaeoecology here has demonstrated potential to elucidate the long-term processes and interactions governing 'palaeo-invasions' (Gillson, 2008; Gillson, 2009) that are relevant in the Cape Flora in the 21st Century. In particular, this study demonstrates the importance of long-term interactions among biota and disturbance in altering the location and proximity of ecosystem state thresholds (see Briske, et al. 2008; Holling, 1973; Lewontin 1969; Scheffer, et al. 2001).

When comparing between and within biome dynamics at Platbos, it is notable that these environmental changes surrounding the 1545 cal yrs BP transition did induce a state shift within fynbos, but not between fynbos and forest. Taxa within the fynbos biome are phytochorologically, phylogenetically and ecologically more akin than those between the fynbos and forest biomes (Bergh, et al. 2014; Colville, et al. 2014; Onstien, et al. 2014; Potts, et al. 2015; Verboom, et al. 2014). In terms of resilience theory, this in effect reduces the energy required to reach the transition threshold, while multiple simultaneous perturbations to the system (i.e. seasonal aridity, increased biomass consumption by large herbivores, and reduced fire) proved sufficiently powerful perturbations to drive change from one basin of attraction to another. Further, given that the Proteaceae population established sometime prior to the proliferation of *Stoebe*-type, and that both taxa represent comparable functional types, the former may have acted as a 'biotic modifier' (Linder, et al. 2012), potentially acting to facilitate invasion by *E. rhinocerotis* through modification of environmental filtering processes. This further illustrates the importance of life-history traits in determining the capacity of an ecosystem to resist invasion.

5.4.1. Future Scenarios

Climate in the GCFR could be 1-3^{o}C warmer by 2100 (Engelbrecht, et al. 2009; Hewiston and Crane, 2006; Tadross, et al. 2005). Associated rainfall modelling has

also suggested that an increased intensity of the sub-tropical easterly moisture-bearing system might result in an increased precipitation amount in this eastern region (Hewiston and Crane, 2006). Although warming at the end of the neoglacial was of differing magnitude and rates to those predicted (~2.5 ^{o}C/ ~400 yrs, or + ~1.25 ^{o}C / ~200 years relative to present; see Talma and Vogel, 1992), associated environmental changes of a similar nature and direction could be expected in the future. The results here reflect predictions and contemporary observations that increasing temperatures lead to increased fire frequency in the east coastal region of the fynbos biome (Southey, et al. 2009). Further, it is indicated here that a future combination of increased temperature, an equitable rainfall regime, and frequent fire, might lead to the development of grassy fynbos that is resistant to colonisation by slower-growing woody fynbos species.

At present in the fynbos biome, one of the greatest threats to fynbos resistance of afrotemperate forest expansion is fire suppression. (Masson and Moll, 1987; van Wilgen, et al. 2012; Poulsen and Hoffman, 2015). Records from Platbos are interrupted by around 50 cal yrs BP/ AD 1900 where fynbos was cleared for pine plantation (Adamson, 1938; Phillips, 1930) and therefore the effects of recent warming in the 20th and 21st Centuries cannot be studied here. However, it is apparent from other, much longer palaeoecological records, that contemporary forest expansion into fynbos may represent an interruption of a multi-million year ecological and evolutionary process (DuPont, et al. 2011; Quick, et al. 2014; Verboom, et al. 2014) of selection for species traits driven by climate, fire and subsequent niche construction in the fynbos biome.

6. SYNTHESIS AND CONCLUSIONS

The central aim of this thesis was to assess the resilience of fynbos to changes in climate, fire and land use at its semi-arid and temperate distribution limits (Chapter 1.3). In order to do so, the palaeoecological histories of the fynbos/ succulent karoo (semi-arid) and fynbos/ afrotemperate forest boundaries have been studied. The analysis of high resolution pollen, spore and charcoal profiles has allowed reconstruction of changes in climate, fire, herbivory and their interactions, and radiocarbon dating facilitated integration of these trends with previously published mid- to late-Holocene palaeoenvironmental records. These data illustrated where and why fynbos exhibited differing resilience properties at its respective boundaries in relation to abiotic, biotic and disturbance phenomena, at both within- and between - biome scales. This chapter considers the findings established in Chapters 4 and 5 within the empirical and theoretical frameworks established in the context of the literature earlier in the thesis (Chapters 1 and 2).

Understanding of biome resilience is imperative in order to assess where, how and why ecosystems might shift, collapse or reform in the face of future climatic change, land-use patterns and associated fire regimes (Connell and Ghedini, 2015; Nimmo, et al. 2015; Oliver, et al. 2015). This is particularly important in the megadiverse fynbos biome and wider Greater Cape Floristic Region (GCFR) which hosts phenomenal levels of biodiversity and endemism but is also under threat from Global Change (Altweg, et al. 2014; Raimondo, et al. 2009). Resilience in the Greater Cape Floristic Region has primarily been applied as a general concept in previous palaeoecological studies (e.g. Quick, et al. 2011; Valsecchi, et al. 2013). Assessment of fynbos resilience to environmental change with respect to its two components - resistance and recovery (Hodgson, et al. 2015) - is wanting with respect to the fynbos biome. The approach adopted here explicitly addresses this research gap.

The two biome boundaries that were selected have polarising characteristics with respect to their contemporary climatic templates and community organisation patterns. By studying semi-arid and temperate boundaries of the fynbos biome this

thesis contextualised the study in relation to global change, local disturbance patterns and ecological interactions. Both boundaries delimit fire prone and fire intolerant biomes, and represent significant contrasts in biome form and function (Bergh, et al. 2014). In particular, the ecosystems at the semi-arid may be expected to have water resource and associated growth limitations, which is less likely to be the case at the temperate biome (Coetsee, et al. 2015; Lechmere-Oertel and Cowling, 2001). The sites also occur in the absence of strong substrate contrasts (Chapter 3), and so enhance expression of the impact of changes in dynamic drivers such as climate. Further, the two specific fynbos GCFR boundaries selected for this thesis contrast substantially in phylogenetic turnover (Bergh, et al. 2014; Verboom, et al. 2009), which emphasises the role of biomes as selective ecological filters the role of evolutionary histories in influencing ecological resilience. The two boundaries therefore provide excellent natural laboratories to examine fynbos palaeoecological resilience with respect to resistance and recovery.

6.1. SUMMARY OF BIOME ORGANISATION AT THE SEMI-ARID AND TEMPERATE BOUNDARIES

6.1.1. The Fynbos-Succulent Karoo Ecocline at Groenkloof

From 5,500 to around 735 cal yrs BP, vegetation at the fynbos-succulent karoo boundary in the Kamiesberg responded to changes in climate and fire. During the relatively mesic phase between 5,500 cal yrs BP, warmer temperatures than present resulted in enhanced summer moisture delivery associated with the subtropical easterlies. Through reduced summer moisture deficit, increased biomass productivity and frequent lightning for ignition, vegetation at the boundary was dominated by fynbos. The fynbos community was of mixed functional composition, characterised by overturning of obligate and facultative seeders (i.e. both fire-dependant and fire independent recruiters). However, between 4,000 can 735 cal yrs BP, cooling and increased summer aridity associated with intensification of the South Atlantic Anticyclone (SAA) resulted in reduced biomass production, fire inhibition and substantially reduced fynbos abundance (Chapter 4). From 735 BP to present, human land use interacted with fire and climatic drivers.

It has been suggested that succulent karoo might invade fynbos where fire is excluded from the latter (Esler, et al. 2015; Rebelo, et al. 2006; Wilson, et al. 2015). This was not the case at Groenkloof. Rather, the resulting community was dominated by Asteraceae and Poaceae, and was not recognisable in the pollen spectra as typical of either succulent karoo or fynbos (Bergh, et al. 2014; Meadows and Sugden, 1991). It may therefore represent a no-analogue community (Williams and Jackson, 2004). This fluid dynamic is characteristic of Gleasonian community organisation (Curtis, 1959; Gleason, 1939; Whittaker, 1975) where individualistic species tolerances prevail and biome cohesion is weak. Where this type of organisation prevails, plants, communities and ecosystems tend to mix-up through time and across environmental gradients (Collins, et al. 1993; Curtis, 1959; Jackson, 2006; Whittaker, 1975).

Later in the record at Groenkloof, climate ameliorated, becoming more mesic from 735 cal yrs BP, reflecting enhanced winter rainfall associated with cooler temperatures and intensification of the westerlies system. At the same time, the first evidence of Khoi pastoralism in the area from around 740 cal yrs BP (Webley, 2007) is associated with increased large herbivore abundance, as indicated by Sordariaceae spore influx and manipulation of the fire regime (Chapter 4). This led to reductions in all but the most disturbance-adapted taxa (*Muraltia and E. rhinocerotis*), and development of a functionally and taxonomically depauperate ecosystem state.

The renosterveld biome is another constituent GCFR which is phytochorologically intermediate to fynbos and succulent karoo (Colville, et al. 2014), and is characterised by similar structural and functional attributes to fynbos (indeed, until recently it was considered a sub-type of the fynbos biome) (Bergh, et al. 2014; Rebelo, et al. 2006). Within renosterveld there is a commonly recognised state shift involving transition from a grass-rich state with frequent fire, to a grass-poor state dominated by the unpalatable shrub *Elytropappus rhinocerotis* (‘renosterbos’) (Levyns, 1956; Rebelo, et al. 2006). The state is known to be highly resistant and maintained through negative feedback processes (Cowling, et al. 1986; Radloff, 2008; Slingsby, et al. 2014). Invasion and dominance of *E. rhinocerotis* is observable elsewhere in the GCFR, in particular in the fynbos biome. It appears that the state shift at Groenkloof represents

a similar phenomenon, reflecting the prevalence and sensitivity of this taxon of a common weed and undesirable ecosystem engineer.

Alternative stable states are by definition maintained by negative feedbacks (Scheffer, et al. 2001; Beisner, et al. 2003). As such, they exhibit homeostatic properties akin to the 'super-organism' perspective offered by Clementsian theory of community organisation (Connell and Ghedini, 2015; Clements, 1936; Scheffer, et al. 2001). This contrasts with Gleasonian-type ecosystem dynamics which represent systems in which few if any internal stabilising forces affecting the system (Holling, et al. 2002). It seems therefore that land-use change (i.e. frequent burning with livestock grazing), interacting with climate change, caused vegetation at the fynbos-succulent karoo ecocline to become more Clementsian in its organisation and dynamics (i.e. species interacted with abiotic and disturbance parameters to maintain temporal stability, rather than being transient assemblages of species responding to individual environmental optima) (Connell and Ghedini, 2015).

Through the entire course of the record at Groenkloof the system appeared to respond elastically, changing significantly following perturbation (i.e. increased aridity) but subsequently restoring its original character with respect to the dominance of fynbos, succulent karoo and the [possible] no-analogue Asteraceae-Poaceae community. Comparison between regional climate dynamics with local hydrological conditions and vegetation suggests that that the system tracked regionally driven Holocene climate dynamics, fynbos being most abundant in association with year-round wet conditions of the Mid-Holocene Altithermal (Heaton, et al. 1983; Talma and Vogel, 1997) between 5500 and 4000 cal yrs BP, declining from 4000 to 735 cal yrs BP as a result of intense summer aridity during the neoglacial (Jerardino, 1993), and subsequently recovering in response to winter-wet Little Ice Age (Weldeab, et al. 2013) from around 735 cal yrs BP onwards. The system can therefore be viewed as resilient through recovery (Oliver, et al. 2015), this recovery being dependant on extrinsic forcing (Nimmo, et al. 2015) whereby the system tracks regional climate dynamics. This thesis therefore indicated that fynbos at its semi-arid boundary at Groenkloof is particularly vulnerable to future climate change.

6.1.2. The Fynbos-Afrotemperate Forest Ecotone at Platbos

The fynbos– afrotemperate forest boundary at Platbos appears to have been remarkably stable over the past approximately 3,000 years. Despite substantial changes in climate, no significant change in the ratio of fynbos to forest occurred at the boundary. Forest and fynbos are alternative stable states (Keeley, et al. 2012) and it is widely held that stability is attributable to consistent fire in fynbos, which precludes invasion and establishment of fire-sensitive forest species (Geldenhuys, 1994; Rebelo, et al. 2006). However, the palaeoecological approach adopted here revealed that invasion of fynbos by forest at Platbos is in fact restricted by more complex mechanics involving a dynamic set of interactions among abiotic, biotic and disturbance parameters. For example, during a period of increased summer aridity (2,800-2,400 cal yrs BP), productivity and ignition were limited in fynbos, leading to high fire-free intervals. This potentially provided an ecological opportunity for fire-sensitive forest pioneers to invade fynbos. However, forest pioneers are sensitive to intense summer drought in open fynbos (Coetsee, et al. 2015; Manders, 1990, 1992) restricting their capacity to establish in fynbos habitat despite the absence of fire. In contrast, during climates associated with summer moisture, such as between 2,400 and 1,800 cal yrs BP, forest pioneers could grow more rapidly but frequent fire in fynbos restricted their opportunity to establish.

At the within-biome scale, significant ecosystem structural, functional and compositional changes occurred in response to these environmental changes. From 2,975 to 1,800 cal yrs BP, increasing temperatures resulted enhanced summer rainfall, resulting in more frequent fire and the development of a herbaceous-grassy fynbos. Subsequently, increased herbivory from around 1,800 cal yrs BP associated with Khoi pastoralists, and a shift towards seasonally-arid winter rainfall, interacted with fire to promote a transition to woody-Proteoid fynbos. Through a succession of taxa, this transformed state came to be dominated by *E. rhinocerotis* and appeared to be resistant to change in response to reinstatement of summer-wet conditions. This scenario bears strong resemblance to the state shift recorded at Groenkloof. It appears therefore that the presently pervasive alternative stable state dominated by renosterbos

has prevailed across the GCFR for many centuries as a result of interactions among livestock, climate, fire and vegetation.

Intriguingly, the state shift at Platbos may have been initiated sometime earlier by increased summer aridity and/ or livestock and the proliferation of Proteaceae centuries earlier from around 1850 cal yrs BP. Both these environmental stressors would favour Proteaceae and, in doing so, alter the fire and disturbance regime in favour of conditions suitable for other taxa with similar traits, acting as a 'biotic modifier' or 'ecosystem engineer' (Linder, et al. 2012). Palaeoecology here has demonstrated potential to elucidate the long-term processes and interactions governing 'palaeo-invasions' and shifts between alternative stable states (Gillson, 2008; Gillson, 2009) that are relevant in the Cape Flora in the 21st Century.

6.1.3. Summary of the Semi-Arid and Temperate Boundaries

In summary, at the semi-arid boundary, aridity has tended – for most of the past 5,500 years – to dominate ecosystem dynamics. This resulted in fluid ecosystem dynamics where partitioning between and coherence among the biomes appeared weak (Gleasonian-type assemblages). In contrast, biotic and disturbance processes dominate at the temperate margin of fynbos, resulting in cohesive, Clementsian-type ecosystem that are highly resistant to environmental change. This agrees with general observations that ecosystems in regions of scarce resources are often dominated by abiotic stress (in this case water scarcity at the semi-arid boundary), while in regions of ample resource availability biotic interactions and disturbance tend to become more deterministic in ecosystem dynamics. This latter case is exemplified by the interactions between fire and rainfall seasonality at the temperate boundary revealed in this thesis (Brown 1995; Darwin, 1859; Dobzhansky 1950; Louthan, et al. 2016; MacArthur 1972; Merriam, 1894; Schimper, 1903; Walter, 1971; von Humboldt, 1807).

At the within-biome scale, at both semi-arid and temperate distribution limits of the fynbos biome, land-use change associated with the activities of Khoi pastoralists appears to have contributed – interacting with changes in the fire regime and possibly climate – to the development of a resistant alternative stable state dominated by the

native invader *E. rhinocerotis* (‘renosterbos’) (Cowling, 1986; Levyns, 1956; Radloff, 2008; Slingsby, et al. 2014). This, firstly, highlights the spatial and temporal pervasiveness this well-known degraded state. Secondly, this provides evidence to support the prevailing understanding that a combination of drivers are required to induce an ecosystem state shift (Willis, et al. 2010). Further, the examples provided here highlight the potential role of palaeoecology in understanding ‘palaeo-invasions’ (Gillson, 2008, 2009) and the role of indigenous species as biotic modifiers (Linder, et al. 2012).

The resilience/ resistance of the fynbos boundary that has been uncovered in this thesis may be surprising in the light of previous predictions, which suggested that the fynbos biome will be especially vulnerable to changing climate (Bomhard, et al. 2005; Hannah, et al. 2005; Midgley, et al. 2002, 2003; Rutherford, 2000). However, the contrasting types and degree of resilience between the fynbos-afrotemperate forest ecotone and the fynbos-succulent karoo ecocline can also be explained in phylogenetic and evolutionary terms.

Members of particular biomes tend to have shared evolutionary histories and associated life history traits, which collectively results in niche construction (Linder, et al. 2012; Potts, et al. 2015). Therefore, biomes (or members of biomes) that evolved under similar conditions should possess traits making between-biome colonisation or transition more likely. Taxa within the fynbos and succulent karoo biomes are phytochorologically, phylogenetically and ecologically more akin than those between the fynbos and forest biomes (Bergh, et al. 2014; Colville, et al. 2014; DuPont, et al. 2011; Onstien, et al. 2014; Potts, et al. 2015; Verboom, et al. 2014). Thus, it could be argued that the high fluidity of the fynbos-succulent karoo ecocline relative to the fynbos-afrotemperate forest ecotone reflects comparative evolutionary histories of the respective biomes. Through the entire record at Platbos, strong internal feedback processes are prevalent at the fynbos-forest boundary (even preceding Khoi pastoralist impacts). In comparison no intrinsic feedbacks were apparent at the within biome scale at Groenkloof (until the anthropogenic state transition). Thus the causal factor differentiating the semi-arid and temperate boundaries appears to be resource availability and disturbance dynamics.

6.2. RESPONSE OF THE FYNBOS BIOME TO CLIMATE CHANGE

Early biome distribution models have predicted high sensitivity and broad (bio-) geographic responses of fynbos to potential future climate scenarios (Bomhard, et al. 2005; Hannah, et al. 2005; Midgley, et al. 2002, 2003; Rutherford, 2000). However, changes of a comparable nature do not seem to be occurring yet. In contrast, more recent projections employing bioclimatic species niche approaches suggest that localised shifts and reshufflings of species will occur (Driver, et al. 2012), requiring understanding of local rather than regional processes (Gillson, et al. 2013). Previous palaeoecological studies in the Cape Floristic Region suggest little change in response to climate since the Last Glacial Maximum at the between-biome scale (Meadows and Sugden, 1991, 1993; Meadows, et al. 2010; Valsecchi, et al. 2013; Quick, et al. 2011, 2015).

It has yet to be determined whether high fynbos resilience reflects continued recovery through climatic buffering of mesic mountain refugia, high physiological resistance to drought, or a combination of these two factors (Altweg, et al. 2014; Verboom, et al. 2009). This thesis has highlighted the prominent the roles of both these mechanisms in maintaining the long-term resilience of fynbos. Previous palaeoecological studies pertaining to fynbos-succulent biome dynamics in the Cederberg mountains (Meadows and Sugden, 1991, 1993; Meadows, et al. 2010; Valsecchi, et al. 2013; Quick, et al. 2011) and fynbos-forest dynamics in the southern Cape (Quick et al 2015) have shown that fynbos has remained resilient at the between-biome scale since the Last Glacial Maximum (LGM). This resilience was afforded by internal adaptation through overturning among fynbos sub-types with varied capacities for resistance to climate and fire (e.g. mesic, frequent-fire loving ericaceous fynbos verses drought-tolerant, slower maturing proteoid fynbos) (Valsecchi, et al. 2013).

In contrast, by locating this study directly within the present-day transition zone between fynbos and succulent karoo, in particular where substrate contrasts were not apparent (Anderson, 2008), fynbos ecological dynamics were emphasised. This allowed clear identification of the recovery process, whereby fynbos abundance (and fire) at its boundary closely responded to regional climate dynamics, which in turn

favoured moist conditions during both warm and cool temperature extremes of the present interglacial. Similarly, at the temperature boundary, the study showed the importance of internal ecological dynamics in stabilising the fynbos forest boundary during climatic changes. Obtaining high resolution data directly from the present-day ecotone at Platbos was key to revealing the dynamic mechanism promoting resistance. Moreover, detailed qualitative consideration of autecological and physiological characteristics of taxa and their ecological interactions at the ecotone was essential in identifying complex dynamics in a system that otherwise might have appeared stable (see Connell and Ghedini, 2015).

At both the semi-arid and temperate ecotones, the data from Groenkloof and Platbos suggest that warmer climate than present was associated with persistence of fynbos and the proliferation of frequent fire under mesic conditions with low summer aridity. This seems surprising given predictions that warmer temperatures of the coming century will result in contraction of fynbos bioclimatic envelope and associated substantial species losses (Bomhard, et al. 2005; Hannah, et al. 2005; Midgley, et al. 2002, 2003; Rutherford, 2000). While this may be true for the true Mediterranean climate regions of the GCFR, it is apparent that eastern ecoregions – more specifically, those associated with the year-round rainfall zone – may benefit from reduced aridity stress under the influence of enhanced easterly flow in summer. Indeed, present projections indicate that winter rainfall will likely be reduced leading those areas in the heart of the current winter rainfall zone (WRZ) to become drier overall (Altweg, et al. 2014), while in areas associated with the year-round rainfall zone (YRZ), decreases in winter rainfall may be offset by increases in summer rainfall as the present summer rainfall zone (SRZ) is expected to become wetter (Altweg, et al 2014; Engelbrecht, et al. 2009; Hewiston and Crane, 2006; MacKellar, et al. 2007). West-east and north-west bioclimatic conditions in the GCFR may therefore be to some extent polarised across future climatic trajectories.

It has also been suggested, in this study (Chapters 4 and 5) as well as in the literature (Quick, et al. 2011; Valsecchi, et al. 2013; West, et al. 2012) that functional overturning at the within-biome scale might afford resilience to fynbos. Certain taxonomic and functional groups have been indicated as particularly resistant to

drought. Indeed, at the succulent karoo boundary at Groenkloof, aridification between 4,000 and 735 cal yrs BP did not result in a reduction in the majority of any woody fynbos taxa, and some such as *Cliffortia* even proliferated. The findings of this study therefore support the main findings with respect to (eco-) physiological research on drought resistance in fynbos (Agenbag, et al. 2007; Altweg, 2014; Mustart, et al. 2012; West, et al. 2012), namely that responses to drought are highly variable among co-occurring species; and that woody plants tend to be highly resistant to drought. Similarly at Platbos (forest boundary), woody Proteaceae, *Stoebe*-type and *Cliffortia* 2 replaced herbaceous grassy fynbos in part at least in response to the impacts of summer drought. This latter finding, as well as the importance of summer and winter rainfall proportion highlighted in this study more generally, supports the view that seasonality of drought is the primary factor determining drought response (Altweg, et al. 2014; West, et al. 2012).

6.3. CONCLUSION

The fynbos biome has expressed contrasting patterns of resilience at its semi-arid and temperate boundaries with succulent karoo and afrotemperate forest, respectively. At the semi-arid distribution, biome organisation was responsive to climate change and tended to be looser, particularly where climate was more arid and fire inhibited. This resulted in the temporary formation of a no-analogue ecosystem dominated by neither typical fynbos nor succulent karoo. Instead, a fluid plant formation dominated by Asteraceae and Poaceae prevailed. Once climate ameliorated, however, fynbos and fire proliferated. The semi-arid fynbos boundary was therefore identified as resilient through recovery. In contrast, ecosystem dynamics at the temperate boundary were dominated by internal feedback processes that promoted between-biome stability, and less visible sensitivity to climate change at the between biome level. Processes that counter disturbance are often invisible to the (palaeo-) ecologist but are fundamental to the understanding of resilience mechanisms. In this study, the careful analysis of autecological assemblages in the context of long-term environmental change allowed the mechanics supporting resilience through resistance to be identified.

At the within-biome scale, both sites manifest impacts of pastoralism during the past 1,500 years which. Through interactions among herbivory, fire, and climate, land-use change promoted the development of alternative stable states within fynbos. These ecosystem states were comparable to the known state shift involving grasses and *E. rhinocerotis* in the renosterveld biome, highlighting the pervasive and prolific impact of the species as a palaeo-invader and undesirable ecosystem engineer.

This thesis has made a significant contribution to the understanding of fynbos resilience by explicitly investigating the expression of resilience through resistance and recovery, which has so far been lacking in the fynbos biome and wider GCFR. The relevance of the findings have been amplified by framing the study within a bioclimatic and theoretical framework that is relevant to contemporary and future environmental and ecological change in the GCFR. Moreover, by identifying when, where and why abiotic, biotic and disturbance parameters become more/ less significant provides important fundamental information regarding how this and other Mediterranean-type biomes might respond to potential future local and global-scale environmental changes. Further work to test the relevance of the frameworks developed here in the fynbos biome and potentially even other Mediterranean-type ecosystems would be of substantial value to the understanding of global biogeography and ecology.

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APPENDIX 1

THE NATURE OF THE EXTANT PLANT COMMUNITY AT GROENKLOOF

Introduction

This section looks to characterise the nature of the plant communities across the fynbos/ succulent karoo biome transition at Groenkloof, the topographic basin containing the wetland from which the Groenkloof 3 sediment core was extracted. This will aid in interpretation of the associated palaeoecological record. Particular attention is paid to the distribution of the key taxa identified in the pollen record.

Study Area

A detailed description of the study site is provided in Chapter 3. Briefly, the Kamiesberg is distributed at the northern extremity of the Fynbos biome's distribution. Fynbos in the Kamiesberg occurs only at the highest altitudes forming 'islands' of fynbos within a matrix of succulent karoo vegetation. Although a general transition from Succulent Karoo to Fynbos is evident along a gradient of increasing altitude, vegetation cover is patchy and overturns rapidly across the landscape, alternating between dominant succulent and non-succulent shrubs and sub-shrubs, Poaceae and Restionaceae (Plate 1, 2, 3). Patches dominated by succulents occur at all altitudes associated with fire-free rocky areas and shallow, skeletal soils. Elements of renosterveld and fynbos occur at higher altitudes in wetter areas such as at seeps.

Methods

A total of 36 quadrats were surveyed within the topographic basin associated with Groenkloof. These quadrats were distributed along three transects spanning varied altitudinal and topographic gradients. The first consisted of 14 quadrats distributed along SE-NW gradient and spanned altitudes between 1059 m and 1578 m (the core GK3 was extracted at around 1200 m asl; Plate 2). A second was composed of 12

quadrats running along a SW-NE transect with plots distributed along an altitudinal gradient between 1201 m and 1578 m. An additional transect running in a S-N direction between 1200 m and 1371 m composed of 10 quadrats was surveyed in order to ensure comprehensive survey of all observable major vegetation patches.

Quadrats sized 5 x 10 m were distributed at approximately 300 m intervals along these transects, though their exact location was biased towards inclusion of qualitatively identified vegetation patches within the landscape. Dominant taxa were identified to at least generic level and their abundances were recorded as percentage of total vegetation cover. Percentage vegetation cover, rock and litter cover were also recorded. Soil depth was measured by hammering a metal rod into the ground along 3 x 5 m transects dissecting the quadrats, and the depth was taken as the average of these measurements.

Figure 1: Mountain top at Groenkloof, ~1560 m asl. Succulents such as Lampranthus *sp. and* Ruschia *sp. dominate in the foreground alongside grasses; adjacent in the background fynbos dominated by Restionaceae.*

Figure 2: View looking East across Groenkloof , ~1200 m asl (light green vegetation indicates location of wetland). The vegetation is dominated by Elytropappus rhinocerotis.

Figure 3: Lowland vegetetation to south of Groenkloof on commercial livestock farm (~1060 m asl.) Vegetation is dominated by Odera *sp.,* Dimorphotheca *(Asteraceae)* Aspalathus *sp..*

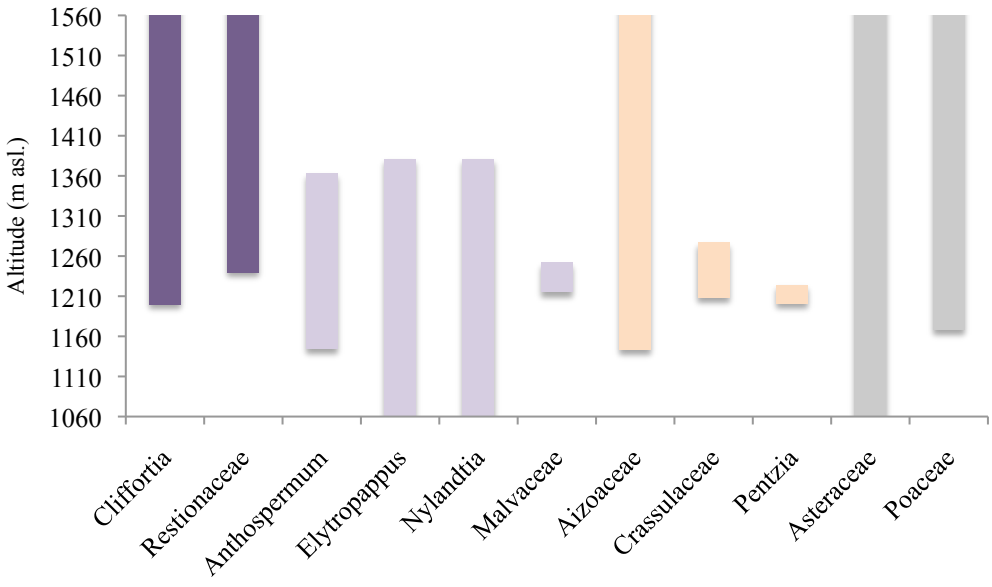

Figure 4: Altitudinal distribution of species within Groenkloof. Dark purple taxa are members of 'pure' fynbos; light purple are members of other fynbos biomes (including Renosterveld and Sandveld); Beige represents Succulent Karoo.

Main findings

The three transects surveyed contained 34 plots in total. They were distributed between altitudes of ~1060 m asl at just beyond the Groenkloof basin to the south and ~1580 m asl to the northeast at the peak of Johanneseberg. Slope aspects covered north, east, south and west and slope angles ranged between 0o and 35o. Land use was predominantly peripheral to designated grazing areas, situated between commercial livestock farms to the south and communal livestock enclosures to the north. Of the plots, four were located on commercial farms to the south while, two were located on communal land and the remainder were in the intermediate zone.

Typical "pure" Fynbos elements Cliffortia ruscifolia and Restionaceae are confined to higher altitudes above ~1250 m (Table 1; Figure 4) where temperature hence water stress are relatively low (Anderson, 2008). C. ruscifolia has been shown as less tolerant of aridity stress than members of the Succulent Karoo (Jacobsen, et al. 2009), and both taxa are very rare at locations receiving MAP below ~250-200 (see probability density functions in: Quick, et al. 2011). This supports the prevailing view

that expansion of Fynbos into Succulent Karoo habitat is limited by relatively low tolerance of aridity stress (Agenbag, et al. 2008; Lechmere-Oertel and Cowling, 2001).

Elytropappus rhinocerotis was highest in abundance at mid-elevations in the Groenkloof basin between ~1150 and 1400 m asl (Table 1, Figure 4). It is known to occupy the intermediate climate space between Succulent Karoo and Fynbos in mountainous areas of the Cape Floristic Region (Agenbag, et al. 2008; Rebelo, et al. 2006). At such altitudes pure Fynbos taxa such as *Cliffortia* and Restionaceae are likely to possess reduced competitive ability due to physiological stress, allowing E. rhinocerotis to prosper where it receives ample rainfall to outcompete slow growing karroid elements for moisture and light (Lechmere-Oertel and Cowling, 2001).

Kamiesberg Mountain Renosterveld (and Renosterveld vegetation in general) is commonly associated with the prevalence of *E. rhinocerotis* and a grassy understory (Rebelo, et al. 2006; Cowling, 1995). Surprisingly, Poaceae was not identified as particularly abundant at Groenkloof, and no clear relationship could be observed between Poaceae and E. rhinocerotis (Table 2; Figure 2). Species of Poaceae where most abundant in Groenkloof at high altitude (~25 % of total vegetation cover; Table 1).

The distributions of leaf-succulent species of the Aizoaceae family (predominantly *Ruschia robusta* and *Lampranthus schulzii*) were not constrained by altitude within Groenkloof (Plate 1; Table 2; Figure 1), suggesting that climatic factors are not dominant constraints on their growth and persistence. It has been argued that expansion of succulent shrubs into Fynbos habitat is inhibited by the prevalence of fire in Fynbos as succulent shrubs are fire intolerant (Rebelo, et al. 2006). The data collected at Groenkloof do not support this assertion, as Aizoaceae species were not confined to fire free microhabitats. Both *R. robusta* and *L. schulzii* were recorded in areas with little or no percentage rock cover (Table 1). Almost all Aizoaceae recorded were situated on shallow soils (</= 30 cm) and have very shallow root systems (Shiponeni, et al. 2011); therefore it appears that soil depth may influence competitive interactions.

Lower altitude sites in Groenkloof are generally characterised by higher proportions of Asteraceae (Table 1), but was widely distributed and abundant within Groenkloof irrespective of biome associations. The prevailing types of vegetation at present are Kamiesberg Mountain Fynbos, Namaqualand Granite Renosterveld (Fynbos biome) and Kamiesberg Mountain Shrubland (Succulent Karoo biome), and all are described as asteraceous shrublands. Lower altitude sites (hence, more arid) were characterised by the prevalence of woody shrubs associated with Succulent Karoo including *Pentzia incana* and *Eriocephalus* spp. (Hoffman, et al. 2009; Rebelo, et al. 2006). Annuals such as *Dimorphotheca* spp. were also more prevalent at lower altitudes, perhaps in association with greater livestock impacts

APPENDIX 2

Depth	age	mura	Clif	rest	stoe	Anth	ruta	faba	malv	clut	asls	poac	irid
0	-50	48,4	3,3	1,6	16,6	2,2	3,3	0,5	3,8	1,1	5,2	1,6	2,2
4	74	32,4	1,1	2,7	24,1	5,8	0,5	2,1	0,0	1,6	7,4	2,7	0,0
8	148	28,7	1,1	1,1	20,5	6,2	2,2	1,1	1,7	1,1	9,3	1,7	2,2
12	222	56,4	1,7	0,0	13,7	4,6	1,1	0,6	0,6	0,0	8,8	4,6	0,0
15	278	58,7	0,0	0,5	19,7	12,1	0,0	0,5	2,4	0,0	2,7	0,5	0,0
20	371	58,8	0,6	2,2	16,2	2,2	0,6	0,0	0,0	0,0	6,4	7,3	0,0
24	445	75,9	8,0	0,0	2,9	1,6	0,0	0,0	0,0	0,5	4,2	0,5	0,0
28	519	63,2	11,7	0,9	4,7	4,5	0,9	0,9	0,0	1,3	5,6	1,3	3,1
32	593	49,7	13,5	0,5	6,8	7,2	0,5	0,0	1,8	1,8	4,3	1,4	0,9
36	667	25,0	27,1	0,5	12,8	4,3	0,5	0,0	0,0	1,1	17,6	4,3	0,0
40	741	15,4	21,0	0,5	14,0	19,6	0,9	0,5	0,5	3,3	6,8	3,7	0,9
44	880	24,4	14,9	1,5	11,7	16,9	0,5	0,0	0,5	1,0	11,2	8,5	0,0
48	1040	26,6	6,1	0,5	14,5	15,0	3,7	0,5	1,4	0,9	9,3	3,3	0,0
52	1201	12,2	6,3	2,6	20,6	22,2	2,6	0,0	1,1	0,5	11,6	5,8	4,2
55	1321	7,1	4,1	1,0	28,3	21,9	3,6	0,5	2,6	1,0	7,4	5,1	0,5
58	1441	12,9	2,6	5,1	15,9	13,4	0,5	0,0	0,0	0,5	17,7	7,7	5,1
60	1521	7,7	12,7	3,3	12,2	18,2	0,0	0,0	0,0	0,0	17,1	5,5	0,6
65	1722	12,7	4,4	4,4	14,4	26,3	0,5	0,0	1,0	0,5	12,0	6,8	0,5
67	1802	3,6	12,9	5,2	8,8	13,9	0,5	0,0	1,0	2,1	24,7	9,8	2,6
75	2122	1,0	11,2	2,9	12,7	22,9	0,5	1,0	5,4	0,0	13,9	15,1	0,0
80	2322	1,6	16,6	5,4	11,5	17,7	0,5	0,0	1,6	0,0	17,2	19,8	0,5
85	2523	1,6	10,9	5,7	12,4	18,6	1,0	0,0	1,0	1,0	17,3	20,2	0,0
88	2643	13,8	20,6	3,7	9,3	16,4	0,0	0,0	0,0	0,0	14,0	13,2	0,0
92	2803	14,9	30,8	2,9	7,5	15,4	0,0	0,5	0,0	0,5	14,0	3,4	0,0
95	2923	13,9	32,3	2,7	7,4	24,7	0,0	0,0	0,0	0,0	7,4	1,3	0,0
100	3124	3,4	12,8	7,4	8,6	16,3	0,0	0,0	1,5	2,0	14,0	29,6	0,0
105	3324	0,5	21,1	7,9	15,5	16,7	0,0	0,0	6,4	3,4	9,3	14,7	0,0
110	3524	3,4	12,7	7,4	8,6	16,2	0,0	0,0	1,5	2,0	14,0	29,4	0,0
115	3725	6,3	26,3	9,1	9,5	19,5	0,0	0,0	0,0	0,5	5,2	16,3	0,0
120	3925	14,5	40,6	8,4	6,5	12,6	0,5	0,0	0,9	0,5	9,6	2,3	0,0
124	4046	21,8	45,0	3,5	5,2	12,7	0,0	0,0	0,9	0,9	2,6	1,7	0,0
130	4209	16,5	18,4	4,7	6,6	18,4	0,0	0,0	0,5	0,9	12,1	15,6	0,0
135	4344	55,6	11,0	1,8	8,2	8,4	0,0	0,0	0,0	2,2	4,4	3,5	0,0
138	4426	33,3	23,8	9,5	7,6	10,5	0,5	0,0	0,0	1,0	8,8	2,9	0,0
140	4480	2,9	47,8	9,7	9,2	13,5	0,5	0,5	0,5	0,0	10,1	0,5	0,5
144	4588	29,0	29,5	0,9	10,4	9,7	0,5	0,5	0,9	0,0	4,4	2,8	0,0
150	4751	4,0	36,3	2,5	8,5	18,9	0,0	1,0	2,5	0,5	13,4	5,0	0,0
155	4886	4,2	9,0	6,9	17,5	22,8	0,0	1,1	0,5	0,5	14,1	8,5	0,5
160	5022	16,5	12,5	10,5	10,0	16,5	0,0	2,0	0,0	1,0	11,5	8,5	0,0
165	5157	42,7	3,2	11,5	8,0	15,1	0,0	1,4	0,0	0,9	3,9	6,9	0,0
168	5238	42,7	5,6	7,1	13,7	15,8	0,0	0,0	0,5	0,5	9,9	1,5	0,0
172	5347	27,6	6,4	20,7	10,6	18,2	0,5	0,0	0,0	0,0	11,6	2,5	0,0
179	5536	27,1	7,2	12,2	12,0	22,6	0,5	0,0	0,0	1,4	8,1	2,3	0,0

Table 1. Pollen percentage data for Groenkloof 3. Depth = cm; age = cal yrs BP; mura = Muraltia; rest = Restionaceae; stoe = Stoebe-type; anth = Anthospermum-type; ruta = Rutaceae; faba = Fabaceae; malv = Malvaceae; clut = Clutia-type; asls = Asteraceae long-spine; poac = Poaceae; irid = Iridaceae.

depth	age	aizo	pent	cras	Chen	gera	asph	Undiff 1	Undiff 2	Undiff 3	Undiff 4
0	-50	0,0	3,8	0,5	1,1	0,0	1,1	0,0	0,0	1,0	0,0
4	74	0,5	0,0	1,1	0,5	0,0	0,0	0,0	0,0	0,0	0,0
8	148	0,6	1,1	2,2	0,6	0,0	0,0	0,0	0,0	0,0	0,4
12	222	0,6	0,0	1,1	3,4	0,6	0,0	0,0	0,0	0,0	0,0
15	278	0,5	1,0	0,5	0,0	0,0	0,0	0,4	0,0	0,0	0,0
20	371	1,7	0,0	1,1	2,2	0,0	0,0	0,0	0,0	0,0	0,0
24	445	0,5	0,0	2,1	2,1	0,5	0,0	0,0	0,0	0,0	0,0
28	519	0,0	0,9	0,4	0,0	0,0	0,0	0,0	0,0	0,0	0,0
32	593	2,7	6,8	1,8	0,5	0,0	0,0	0,0	0,0	0,0	0,0
36	667	0,5	0,5	1,1	0,0	0,5	2,1	0,0	0,0	0,0	0,0
40	741	1,9	4,7	0,2	1,4	0,5	0,9	0,0	0,0	0,0	0,0
44	880	0,5	2,5	4,5	0,0	0,0	0,5	0,0	0,0	0,0	0,0
48	1040	2,8	2,3	0,9	0,0	2,8	0,0	0,0	0,0	0,0	1,0
52	1201	0,5	1,1	4,2	0,0	0,0	0,5	0,0	0,0	0,0	0,0
55	1321	2,6	0,0	0,5	0,0	2,0	3,6	0,0	0,0	0,4	0,4
58	1441	1,5	0,0	3,6	2,1	0,0	0,5	0,0	0,0	0,0	0,0
60	1521	0,0	0,6	3,9	2,8	0,0	1,7	0,0	0,0	0,0	0,0
65	1722	4,4	2,9	1,5	1,0	0,0	0,5	0,0	0,0	0,0	0,4
67	1802	3,1	1,5	1,0	1,5	1,0	1,0	0,0	0,0	0,0	0,0
75	2122	7,8	1,9	0,5	1,0	0,0	1,9	0,0	0,0	0,0	0,0
80	2322	3,2	2,1	0,0	0,5	0,5	0,5	0,0	0,0	0,0	0,0
85	2523	2,6	1,6	1,0	2,1	2,6	0,5	0,0	0,0	0,0	0,0
88	2643	2,1	0,0	3,7	1,6	0,5	1,1	0,0	0,0	0,0	0,0
92	2803	1,4	1,4	1,0	2,4	0,5	0,0	0,0	0,0	0,0	0,0
95	2923	0,4	5,4	1,3	1,3	0,4	0,4	0,0	0,0	0,0	0,0
100	3124	1,0	0,0	2,0	0,0	0,5	0,0	0,0	0,0	0,0	0,0
105	3324	1,0	0,5	0,5	0,5	0,5	0,0	0,0	0,0	0,4	0,0
110	3524	1,0	0,0	2,0	0,0	0,5	0,0	0,0	0,0	0,0	0,0
115	3725	3,2	0,9	1,4	0,9	0,5	0,0	0,0	0,0	0,0	0,0
120	3925	1,9	0,0	0,5	0,0	0,5	0,0	0,0	0,0	0,0	0,0
124	4046	1,7	0,0	0,9	0,4	1,7	0,0	0,0	0,0	0,0	0,0
130	4209	0,5	0,0	1,4	1,4	0,0	0,0	0,0	0,0	0,0	0,0
135	4344	2,6	0,0	0,4	0,4	0,0	0,0	0,8	0,0	0,0	0,0
138	4426	1,4	0,0	0,0	1,0	0,0	0,0	0,0	0,0	0,0	0,0
140	4480	0,0	0,0	0,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0
144	4588	4,6	3,7	0,5	0,0	0,9	0,0	0,0	0,0	0,0	0,4
150	4751	0,5	2,5	0,5	0,5	1,0	0,0	0,0	0,0	0,0	0,0
155	4886	2,1	2,1	2,1	0,0	0,0	3,2	0,0	0,8	0,0	0,0
160	5022	2,5	1,0	1,5	0,5	2,5	0,0	0,0	0,0	0,0	0,0
165	5157	2,3	0,5	0,9	0,5	0,5	0,0	0,0	0,0	0,0	0,0
168	5238	1,0	0,5	0,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0
172	5347	0,0	0,5	0,0	1,0	0,5	0,0	0,0	0,0	0,0	0,0
179	5536	1,4	2,3	0,5	0,0	1,4	0,0	0,0	0,0	0,0	0,0

Table 1 (continued). Pollen percentage data for Groenkloof 3. Depth = cm; age = cal yrs BP; aizo = Aizoaceae; pent = Pentzia-type; cras = Crassulaceae; chen = Chenopodiaceae; gera = Geraneaceae; asph = Asphodelaceae; Undiff = Unidentified pollen.

depth	age	Undiff_5	Undiff_6	Undiff_7	Undiff_8	Undiff_9	Undiff_10	Undiff_11
0	-50	0,0	0,0	0,0	0,0	0,0	0,0	0,0
4	74	0,0	0,0	0,4	0,0	0,0	0,0	0,0
8	148	0,0	0,0	0,0	0,0	0,0	0,0	0,0
12	222	0,0	0,0	0,0	0,0	0,0	0,0	0,0
15	278	0,0	0,0	0,0	0,0	0,0	0,0	0,0
20	371	0,0	0,0	0,0	0,0	0,0	0,0	0,0
24	445	0,0	0,0	0,0	0,0	0,0	0,0	0,0
28	519	0,0	0,0	0,0	0,0	0,0	0,0	0,0
32	593	0,0	0,0	0,0	0,0	0,0	0,0	0,0
36	667	0,0	0,0	0,0	0,0	1,6	0,0	0,0
40	741	0,0	1,7	0,0	0,0	0,0	0,0	0,0
44	880	0,0	0,0	0,0	0,0	0,8	0,0	0,0
48	1040	0,3	0,7	1,3	0,0	0,0	0,0	0,0
52	1201	0,0	0,0	0,0	0,0	0,0	0,0	0,0
55	1321	0,0	0,0	0,0	0,0	0,0	0,0	0,0
58	1441	0,0	0,0	0,0	0,0	0,0	0,0	0,0
60	1521	0,0	0,0	0,0	0,0	0,4	0,0	0,0
65	1722	1,9	0,0	0,0	0,0	0,0	0,0	0,0
67	1802	0,0	0,0	0,0	0,0	0,0	0,0	0,0
75	2122	0,0	0,0	0,0	0,0	0,0	0,0	0,0
80	2322	0,0	0,0	0,0	0,0	0,4	0,0	0,0
85	2523	0,0	0,0	0,0	0,0	0,0	0,0	0,0
88	2643	0,0	0,0	0,0	0,0	0,0	0,0	0,0
92	2803	0,4	0,0	0,0	0,0	0,4	0,0	0,0
95	2923	0,0	0,0	0,0	0,0	0,0	0,0	0,0
100	3124	0,0	0,0	0,0	0,0	0,8	0,0	0,0
105	3324	0,0	0,0	0,0	0,0	0,0	0,0	0,0
110	3524	0,0	0,0	0,0	0,0	0,8	0,0	0,0
115	3725	0,0	0,0	0,0	0,0	0,0	0,0	0,0
120	3925	0,0	0,0	0,0	0,0	0,0	0,0	0,0
124	4046	0,0	0,0	0,0	0,0	0,0	0,0	0,0
130	4209	0,0	0,0	0,0	0,0	0,0	0,0	0,0
135	4344	0,0	0,0	0,0	0,0	0,0	0,0	0,0
138	4426	0,0	0,0	0,0	0,0	0,0	0,0	0,0
140	4480	0,0	0,0	0,0	0,0	1,8	0,0	0,0
144	4588	0,0	0,0	0,0	0,0	0,0	0,0	0,0
150	4751	0,0	0,0	0,0	0,0	0,0	0,0	0,0
155	4886	0,4	0,0	0,0	0,0	0,0	0,0	0,4
160	5022	0,4	0,0	0,0	0,0	0,0	0,4	0,0
165	5157	0,0	0,0	0,0	0,0	0,0	0,0	0,0
168	5238	0,0	0,0	0,0	0,0	0,0	0,0	0,0
172	5347	0,0	0,0	0,0	0,0	0,0	0,0	0,0

179	5536	0,0	0,0	0,0	0,0	0,0	0,0	0,0

Table 1 (continued). Pollen percentage data for Groenkloof 3. Depth = cm; age = cal yrs BP; Undiff = Unidentified pollen.

depth	age	gunn	cype	mono	tril	junc	gela	sord	zygn	glom	Ricc
0	-50	18,1	39,5	0,0	1,1	0,7	0,0	6,5	0,4	0,0	0,0
4	74	6,8	9,2	0,2	0,6	0,0	0,3	0,8	0,0	0,0	0,3
8	148	8,1	3,6	0,1	0,3	0,3	0,3	1,2	0,0	0,0	0,1
12	222	7,7	3,9	0,2	2,8	0,0	1,6	0,4	0,0	0,0	0,2
15	278	1,6	3,1	1,4	0,6	1,2	1,0	8,2	0,2	0,0	0,0
20	371	17,3	34,0	0,0	1,7	0,6	4,5	6,1	0,0	0,0	1,1
24	445	0,0	22,2	0,0	11,9	0,5	1,0	3,1	0,0	0,0	0,0
28	519	3,6	8,9	0,4	12,4	0,0	0,0	0,0	0,0	0,0	0,9
32	593	0,0	14,0	0,4	22,5	0,0	1,5	0,0	0,0	0,0	0,0
36	667	0,0	5,4	0,1	18,5	0,1	0,1	0,1	0,0	0,0	0,3
40	741	0,0	5,5	0,0	7,8	0,2	0,0	0,5	0,0	0,0	0,0
44	880	0,7	14,7	0,2	8,6	0,0	0,2	1,1	0,0	0,0	0,2
48	1040	1,1	6,5	0,0	0,0	0,0	0,0	0,2	0,0	0,0	0,0
52	1201	0,7	9,7	0,0	4,7	0,0	0,0	0,7	0,0	0,0	0,2
55	1321	0,0	3,1	0,5	3,8	0,3	0,0	0,0	0,0	0,0	0,0
58	1441	2,3	6,9	0,5	3,1	0,0	0,0	1,4	0,0	0,0	0,8
60	1521	2,7	1,6	0,0	4,8	0,0	0,0	0,4	0,0	0,7	0,1
65	1722	0,0	0,1	0,5	1,0	0,1	0,0	0,0	0,0	0,0	0,0
67	1802	1,3	4,3	0,1	6,2	0,4	0,0	4,0	0,1	0,0	0,8
75	2122	0,0	1,3	0,4	1,3	0,1	0,0	0,0	0,0	0,0	0,1
80	2322	0,9	1,5	0,4	0,6	0,3	0,0	0,1	0,1	0,0	0,6
85	2523	0,0	4,0	0,2	2,7	1,0	0,0	0,1	0,1	0,0	0,0
88	2643	0,8	2,2	0,1	1,2	0,0	0,0	0,0	0,0	0,0	0,3
92	2803	1,9	7,7	0,0	12,6	0,8	0,0	0,0	0,5	0,0	0,0
95	2923	0,0	4,9	0,8	4,9	0,0	0,0	0,0	0,2	0,0	0,2
100	3124	0,0	0,9	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
105	3324	0,0	3,9	0,0	0,4	0,1	0,0	0,1	0,0	0,0	0,1
110	3524	0,0	0,9	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
115	3725	0,0	1,6	0,0	0,4	0,3	0,0	0,0	0,0	0,0	0,0
120	3925	0,6	7,4	0,2	3,1	0,0	0,0	0,0	0,0	0,0	0,2
124	4046	0,0	12,3	0,0	6,2	1,2	3,1	2,5	0,0	0,0	0,6
130	4209	0,9	16,9	0,2	3,3	0,2	0,0	0,0	0,7	0,0	0,2
135	4344	0,0	3,0	0,9	1,5	0,2	0,0	0,0	0,1	0,0	0,0
138	4426	1,8	12,7	0,0	2,9	0,0	0,0	0,7	0,0	0,0	0,0
140	4480	0,5	8,1	0,2	2,4	0,2	0,0	0,0	0,0	0,0	0,0
144	4588	0,0	3,3	0,2	3,3	0,2	0,0	0,0	0,0	0,0	0,0
150	4751	2,6	12,5	0,0	12,5	1,0	1,0	0,5	0,0	0,0	0,5
155	4886	1,2	2,0	0,4	5,0	0,2	0,0	0,0	0,0	0,0	0,8
160	5022	6,0	7,6	0,0	1,6	0,4	0,0	1,2	0,0	0,0	1,6
165	5157	0,0	4,3	0,3	0,4	0,9	0,0	0,3	0,2	0,6	0,0

168	5238	0,9	7,4	0,0	1,3	0,0	0,0	0,0	0,0	0,0	0,2
172	5347	0,5	5,1	0,3	2,2	0,0	0,0	0,0	0,0	0,0	0,3
179	5536	0,0	5,6	2,0	0,5	5,1	0,0	0,0	8,4	0,3	0,8

Table 2. Non-land pollen and non-pollen palynomorph influx rate data (n items/ yr/ 100) for Groenkloof 3. Depth = cm; age = cal yrs BP; gunn = Gunnera; cype = Cyperaceae; mono = Monolete spores; tril = Trilete spores; junc = Juncaceae; gela = Gelasinospora; sord = Sordaricaceae; zygn = Zygnemataceae; glom = Glomus; ricc = Riccia.

depth	age	3-12um	13-25um	3-25um	26-50um	50-150um	3-150um	>150um
0	-50	0,01	0,01	0,02	0,00	0,02	0,07	8
4	74	0,13	0,02	0,15	0,01	0,02	0,32	3
8	148	0,02	0,01	0,02	0,00	0,02	0,07	10
12	222	0,07	0,03	0,10	0,01	0,00	0,22	55
15	278	0,13	0,05	0,19	0,01	0,10	0,48	9
20	371	0,22	0,07	0,29	0,02	0,01	0,62	129
24	445	0,24	0,06	0,30	0,02	0,16	0,77	19
28	519	0,38	0,07	0,46	0,04	0,01	0,97	1
32	593	0,30	0,07	0,38	0,01	0,20	0,97	29
36	667	0,27	0,08	0,35	0,03	0,01	0,74	108
40	741	0,12	0,02	0,14	0,01	0,15	0,43	80
44	880	0,22	0,03	0,25	0,02	0,00	0,52	46
48	1040	0,04	0,01	0,04	0,00	0,05	0,13	10
52	1201	0,26	0,01	0,28	0,01	0,00	0,57	11
55	1321	0,07	0,02	0,08	0,00	0,09	0,25	4
58	1441	0,21	0,02	0,23	0,01	0,00	0,47	64
60	1521	0,11	0,02	0,12	0,01	0,00	0,25	166
65	1722	0,02	0,01	0,03	0,00	0,00	0,06	3
67	1802	0,10	0,01	0,11	0,00	0,00	0,22	8
75	2122	0,04	0,01	0,05	0,00	0,06	0,17	7
80	2322	0,05	0,01	0,06	0,00	0,00	0,11	6
85	2523	0,02	0,01	0,03	0,00	0,03	0,09	2
88	2643	0,02	0,00	0,03	0,00	0,00	0,06	3
92	2803	0,32	0,03	0,35	0,01	0,00	0,72	40
95	2923	0,07	0,02	0,09	0,01	0,05	0,25	13
100	3124	0,00	0,00	0,00	0,00	0,00	0,01	8
105	3324	0,08	0,05	0,13	0,01	0,07	0,36	15
110	3524	0,00	0,00	0,00	0,00	0,00	0,01	17
115	3725	0,01	0,00	0,02	0,00	0,02	0,05	2
120	3925	0,14	0,05	0,18	0,01	0,00	0,38	16
124	4046	0,22	0,14	0,36	0,03	0,10	0,84	141
130	4209	0,63	0,20	0,82	0,07	0,00	1,73	40
135	4344	0,11	0,02	0,13	0,01	0,07	0,32	10
138	4426	0,45	0,07	0,51	0,02	0,00	1,05	27
140	4480	1,80	0,74	2,54	0,29	0,00	5,38	5
144	4588	0,19	0,19	0,38	0,06	0,11	0,93	671
150	4751	0,36	0,08	0,44	0,04	0,02	0,94	62
155	4886	0,36	0,07	0,43	0,01	0,11	0,98	46
160	5022	0,89	0,34	1,23	0,08	0,01	2,55	39

165	5157	0,04	0,02	0,06	0,00	0,06	0,18	5
168	5238	0,17	0,02	0,20	0,02	0,01	0,42	81
172	5347	0,28	0,08	0,36	0,06	0,01	0,80	81
179	5536	0,08	0,06	0,14	0,01	0,08	0,37	25

Table 3. Charcoal for accumulation rate data for Groenkloof 3. Depth = cm; age = cal yrs BP; all size classes >150um are calculated as cm2/ cm3-1/ yr; >150um are fragments/ yr.

depth	age	asls	clif1	clif2	rest	prot	eric	pass	ruta	anth	stoe	poac	cras	berz
0	-50	4,3	0,6	1,8	5,5	2,4	4,3	0,6	0,0	1,8	1,8	7,3	3,0	0,6
6	-15	3,1	1,0	0,0	1,0	0,0	7,2	1,0	0,0	2,1	4,1	6,2	2,1	0,0
14	25	5,4	0,8	1,6	4,7	6,2	10,9	0,8	0,0	2,3	2,3	9,3	3,9	0,0
20	50	6,1	1,5	4,5	1,5	2,3	12,9	1,5	2,3	1,5	5,3	8,3	3,8	0,0
26	90	10,1	4,7	6,0	3,4	10,7	8,7	0,7	0,7	1,3	13,4	5,4	1,3	0,7
28	130	9,8	4,6	8,8	0,4	6,7	4,2	0,0	0,0	0,4	24,2	10,9	0,0	0,4
30	175	9,2	9,2	5,8	0,0	8,5	3,8	0,0	0,0	0,8	32,3	10,4	0,8	0,4
32	285	14,6	2,3	10,3	0,0	12,3	4,6	0,0	0,0	0,0	18,4	11,5	0,8	1,5
34	395	11,0	5,5	10,2	0,0	18,8	2,7	0,0	0,8	1,2	15,7	6,3	0,4	1,6
36	505	12,5	5,5	15,8	2,6	6,3	2,9	0,4	0,0	1,1	12,1	3,7	1,8	0,7
38	615	6,6	2,7	9,3	1,9	31,0	2,7	0,0	0,0	0,4	7,0	9,3	1,2	2,3
40	725	9,7	10,1	4,9	0,7	14,6	5,6	1,1	0,4	1,5	12,0	6,7	0,0	0,4
42	835	20,9	3,5	5,4	1,6	21,7	3,1	0,0	0,0	2,7	10,9	3,5	1,9	0,0
46	1055	13,5	2,6	6,8	0,8	20,3	1,1	0,0	0,0	0,4	21,4	4,1	1,5	0,4
48	1165	10,7	4,6	6,1	1,9	10,0	9,2	0,0	0,0	1,9	14,6	3,4	0,0	1,9
50	1280	10,6	17,4	0,0	0,4	11,3	3,8	1,5	0,0	2,6	10,2	5,7	1,5	3,4
52	1390	13,8	12,7	0,0	1,1	10,5	4,7	0,4	0,0	2,5	12,4	5,1	1,5	2,5
54	1500	12,7	3,1	3,4	2,1	5,2	7,9	0,3	0,0	1,7	13,1	5,8	5,5	0,7
56	1590	7,3	23,6	0,0	1,2	12,0	7,3	0,4	0,0	3,1	3,9	8,5	0,0	3,1
58	1655	9,5	10,6	0,0	0,7	11,7	6,2	0,4	0,0	2,2	4,7	14,2	0,4	3,3
60	1725	6,1	8,3	2,5	1,4	5,0	5,8	0,0	0,4	1,4	0,7	14,0	0,0	3,6
62	1795	6,7	17,2	0,0	0,4	6,7	6,7	0,7	0,0	2,2	0,7	13,8	2,2	3,4
64	1860	9,1	21,1	0,0	1,9	5,7	7,9	0,8	0,0	2,3	0,0	7,9	1,9	3,4
66	1930	13,6	14,0	0,0	4,2	0,4	5,7	0,8	0,4	2,3	0,4	12,1	3,8	2,3
68	2000	9,3	18,5	0,0	1,9	1,1	8,5	0,4	0,0	1,1	1,5	7,8	4,1	5,9
70	2070	12,7	20,1	0,0	2,7	1,9	5,4	0,0	0,4	3,9	1,9	14,7	2,7	8,1
72	2140	14,1	23,6	0,0	1,9	3,4	4,6	0,8	0,0	1,5	0,8	14,1	2,7	3,0
74	2215	13,5	18,2	0,0	3,6	1,5	2,6	0,7	0,0	2,6	1,1	11,7	4,0	2,6
76	2285	12,0	25,1	0,0	7,1	1,1	3,9	1,8	0,0	3,2	1,1	4,6	4,2	8,1
78	2355	13,6	20,4	0,4	4,5	0,8	6,0	1,5	0,0	4,9	2,3	4,2	3,4	9,8
80	2430	11,2	16,2	2,5	2,2	2,5	4,0	0,7	0,0	2,2	1,1	15,9	0,0	1,8
82	2505	17,0	23,0	0,0	1,5	5,3	4,5	3,0	0,0	1,1	2,6	6,8	1,5	10,2
84	2580	9,8	26,9	0,0	1,5	4,9	3,8	3,0	0,0	4,2	4,2	9,5	1,5	10,6
86	2655	11,1	20,4	0,0	4,1	2,6	5,2	1,1	0,0	1,9	0,4	8,9	1,1	3,0
88	2730	9,8	26,9	0,0	1,5	4,9	3,8	3,0	0,0	4,2	4,2	9,5	1,5	10,6
92	2890	8,8	27,7	0,0	3,9	7,4	2,8	2,8	0,0	0,4	0,7	2,8	2,8	12,6
94	2970	9,3	21,3	0,4	3,4	4,1	5,6	0,0	0,0	0,4	3,4	5,6	5,6	6,0

Table 4. Platbos 1 percentage pollen data. Depth = cm; age = cal yrs BP; asls = Asteraceae long spine; clif1 = Cliffortia 1; clif2 = Cliffortia 2; rest = Restionaceae; prot = Proteaceae; eric = Ericaceae; pass = Passerina-type; ruta = Rutaceae; anth = Anthospermum-type; stoe = Stoebe-type; poac = Poaceae; cras = Crassulaceae; berz = Berzelia-type.

depth	age	lami	eben	rhus	dodo	cele	cant	cuno	podo	lora	myca	brac	ilex	olea	oxal
0	-50	3,0	0,0	0,6	0,0	1,2	11,0	0,0	11,6	0,0	0,0	10,4	0,0	0,0	0,0
6	-15	1,0	0,0	3,1	0,0	2,1	15,5	0,0	6,2	0,0	1,0	5,2	0,0	0,0	0,0
14	25	3,1	0,0	1,6	0,0	5,4	11,6	0,0	10,9	0,0	7,0	2,3	0,0	0,0	0,0
20	50	3,0	0,0	1,5	0,0	3,8	8,3	1,5	6,1	0,8	15,2	0,8	0,0	0,0	0,8
26	90	3,4	0,0	0,7	2,0	0,7	5,4	0,0	4,0	0,0	5,4	0,0	0,7	0,0	0,0
28	130	3,5	0,0	1,1	0,4	2,8	3,2	0,0	4,2	0,0	0,7	0,7	0,4	0,0	0,0
30	175	2,3	0,0	0,8	0,0	0,8	7,3	0,8	1,5	0,0	0,0	1,2	0,0	0,0	0,0
32	285	4,6	0,0	0,8	0,4	2,3	4,2	0,0	4,2	0,0	0,8	0,4	0,0	0,0	0,0
34	395	5,9	0,0	1,6	0,0	2,0	5,9	0,0	4,3	1,6	0,0	0,8	0,0	0,0	0,0
36	505	1,8	0,0	4,0	0,0	2,9	4,8	0,4	2,6	0,7	0,4	0,7	0,0	0,0	0,0
38	615	8,5	0,0	1,2	0,0	5,0	1,2	0,0	6,2	0,0	0,0	0,4	0,4	0,0	0,0
40	725	6,7	0,0	0,0	0,0	3,4	3,4	0,0	4,9	1,1	0,0	1,5	0,4	0,0	0,0
42	835	8,1	0,0	2,3	0,0	1,2	3,5	0,0	1,9	0,0	1,2	1,2	0,0	0,0	0,4
46	1055	6,8	0,0	2,6	0,0	0,4	0,4	0,4	6,0	0,0	0,0	2,3	0,8	0,0	0,8
48	1165	2,7	0,0	1,5	0,0	8,4	5,7	1,1	1,1	0,0	0,4	0,0	0,0	0,0	0,0
50	1280	6,8	0,0	1,1	0,4	4,9	5,3	1,1	6,0	0,0	0,0	1,1	0,8	0,0	0,0
52	1390	7,3	0,0	1,1	0,0	4,4	2,2	0,4	8,4	0,0	0,0	0,4	1,1	0,0	0,4
54	1500	5,8	0,0	1,4	0,0	5,2	7,9	0,7	3,1	0,0	2,7	1,4	0,0	1,0	0,3
56	1590	6,2	0,0	1,5	0,0	1,5	6,6	0,4	8,1	0,4	0,0	0,0	0,0	0,0	0,0
58	1655	12,8	0,0	1,8	0,0	1,8	4,0	0,4	4,0	0,7	0,7	0,7	1,5	0,0	0,4
60	1725	6,5	0,0	1,8	0,0	1,8	0,7	0,7	3,2	0,0	2,9	1,1	0,0	1,1	0,0
62	1795	17,5	0,0	3,7	0,0	1,9	3,7	0,0	1,5	0,0	0,7	0,7	0,0	0,0	0,0
64	1860	16,6	0,0	3,0	0,0	1,5	0,0	0,0	3,0	0,0	3,0	0,8	1,1	0,0	0,0
66	1930	11,7	0,4	0,4	0,0	2,3	1,1	0,8	3,4	0,0	2,6	0,8	0,4	1,1	0,0
68	2000	15,2	0,0	2,2	0,0	3,7	2,6	0,0	2,6	0,0	1,1	1,9	1,1	0,0	1,1
70	2070	6,9	0,0	2,7	0,0	3,5	1,5	0,0	3,5	0,0	0,4	0,4	1,2	0,0	0,0
72	2140	7,2	0,0	2,3	0,0	5,3	1,9	0,0	3,0	0,0	0,8	0,8	0,0	0,0	0,0
74	2215	9,5	0,0	2,9	0,0	7,7	1,1	0,0	1,8	0,0	1,5	1,5	0,0	1,1	0,0
76	2285	12,0	0,0	1,1	0,0	3,5	1,4	0,0	3,5	0,0	0,4	3,2	0,7	0,0	0,0
78	2355	9,4	0,0	2,3	0,0	3,0	3,8	0,8	2,6	0,0	0,8	3,0	0,0	0,0	0,0
80	2430	4,3	0,0	1,1	0,0	2,5	1,8	0,7	3,2	0,0	2,9	3,2	0,7	1,1	0,0
82	2505	6,8	0,0	1,9	0,0	3,4	4,5	0,0	2,6	0,0	1,1	2,3	0,0	0,0	0,0
84	2580	4,9	0,0	1,1	0,0	2,3	3,8	0,0	2,7	0,0	2,3	0,8	0,0	0,0	0,0
86	2655	2,6	0,0	4,4	0,0	3,0	0,0	0,4	4,4	0,0	3,7	5,6	0,0	0,4	0,0
88	2730	4,9	0,0	1,1	0,0	2,3	3,8	0,0	2,7	0,0	2,3	0,8	0,0	0,0	0,0
92	2890	4,2	0,0	2,8	0,0	4,2	1,4	0,0	4,2	0,0	0,0	2,5	0,0	0,0	0,0
94	2970	4,5	0,0	3,7	0,0	4,9	3,7	0,0	2,2	0,0	0,7	4,1	0,0	0,0	0,0

Table 4 (continued). Platbos 1 percentage pollen data. Depth = cm; age = cal yrs BP; lami = Lamiaceae; eben = Ebenaceae; rhus = Rhus; dodo = Dodonea; cele = Celastraceae; cant = Canthium; cuno = Cunonia; podo = Podocarpus; lora = Loranthaceae; myca = Myricaceae; brac = Brachylaena; ilex = Ilex; olea = Olea; oxal = Oxalidaceae.

depth	age	alct	thym	faba	poly	rham	irid	Arte	euph	pent	chen
0	-50	0,0	0,6	0,0	0,0	0,6	0,0	1,2	0,0	0,0	0,0
6	-15	0,0	0,0	1,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
14	25	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,8
20	50	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
26	90	0,0	0,7	0,0	0,7	0,7	0,0	0,0	0,0	0,0	0,0
28	130	0,0	0,4	0,0	0,0	0,7	0,4	0,0	0,0	0,0	0,0
30	175	0,0	0,8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
32	285	0,0	0,0	0,4	0,4	0,8	0,0	0,0	0,0	0,0	0,0
34	395	0,0	0,8	1,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0
36	505	0,0	0,0	0,4	0,0	0,0	0,0	0,0	0,0	0,4	0,0
38	615	0,0	0,4	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
40	725	0,0	0,4	0,7	0,0	1,9	0,4	0,0	0,4	0,0	0,0
42	835	0,0	1,2	0,4	0,4	0,4	0,0	0,0	0,0	0,0	0,0
46	1055	0,0	0,8	0,0	0,0	1,5	0,0	0,0	0,0	0,0	0,0
48	1165	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
50	1280	0,0	0,0	0,0	0,0	0,8	0,0	0,0	0,0	0,0	0,0
52	1390	0,0	0,0	0,0	0,0	0,0	1,1	0,0	0,0	0,0	0,0
54	1500	0,0	0,3	0,0	0,7	0,0	0,0	0,0	0,3	0,0	0,0
56	1590	0,0	0,0	0,4	0,0	0,0	0,0	0,0	0,0	0,0	0,0
58	1655	0,0	0,0	0,0	0,0	0,4	0,0	0,0	0,0	0,0	0,0
60	1725	0,0	0,0	0,0	0,0	0,0	0,0	0,4	1,1	0,0	0,0
62	1795	0,4	0,0	0,0	0,4	0,4	0,4	0,0	0,0	0,0	0,0
64	1860	0,0	0,0	0,0	0,0	0,0	0,4	0,0	0,0	0,0	0,0
66	1930	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,4	0,8	0,0
68	2000	0,0	0,0	0,0	0,0	0,0	1,1	0,0	0,0	0,4	0,0
70	2070	0,0	0,0	0,0	0,0	0,0	0,8	0,0	0,0	0,4	0,0
72	2140	0,0	0,0	0,0	0,0	0,0	2,3	0,0	0,0	0,8	0,0
74	2215	0,0	0,0	0,0	0,0	0,0	0,7	0,0	0,4	0,0	0,0
76	2285	0,0	0,0	0,0	0,0	0,0	0,4	0,0	0,0	0,0	0,0
78	2355	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
80	2430	0,0	0,0	0,0	0,0	0,4	0,0	0,0	1,1	0,0	0,0
82	2505	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
84	2580	0,0	0,0	0,0	0,0	0,0	0,4	0,0	0,0	0,0	0,0
86	2655	0,0	0,0	0,4	0,0	0,4	0,7	0,0	1,1	0,4	0,0
88	2730	0,0	0,0	0,0	0,0	0,0	0,4	0,0	0,0	0,0	0,0
92	2890	0,0	0,4	0,4	0,0	0,7	0,0	1,1	0,0	0,0	0,0

94	2970	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,7	0,0

Table 4 (continued). Platbos 1 percentage pollen data. Depth = cm; age = cal yrs BP; alct = Asteraceae lactacoidae; thym = Thymeliaceae; faba = Fabaceae (undiff); poly = Polygalaceae; rham = Rhamnaceae; irid = Iridaceae; arte = Artemisia-type; euph = Euphorbiaceae; pent = Pentzia-type; chen = Chenopodiaceae.

depth	age	cype	myrit	myrip	gune	mono	tril	sord	dama	cnld
0	-50	59,3	1,6	0,0	0,0	14,1	43,7	1,6	51,5	15,6
6	-16	39,3	3,6	3,6	0,0	57,2	64,3	0,0	21,4	10,7
14	26	28,6	4,8	0,0	0,0	1,6	9,5	0,0	11,1	6,4
20	58	15,5	0,0	0,0	0,0	12,4	3,1	0,0	31,0	15,5
26	91	13,9	1,6	0,0	0,0	1,6	2,4	0,0	7,3	1,6
28	132	7,0	15,5	0,0	0,0	2,8	26,7	1,4	7,0	5,6
30	177	5,0	2,8	0,0	0,0	0,0	1,1	0,0	1,7	3,3
32	284	9,9	5,0	0,0	0,0	1,7	3,3	1,7	4,1	5,8
34	395	5,5	0,5	0,0	0,0	1,0	1,0	0,0	1,0	0,0
36	505	3,8	1,4	0,0	0,0	1,9	5,8	0,0	15,8	3,4
38	615	7,6	0,0	0,0	0,0	0,4	1,8	1,8	3,6	0,0
40	726	14,9	1,9	0,6	0,0	0,6	3,9	1,9	29,1	1,3
42	836	3,2	2,1	0,0	0,0	1,1	0,0	3,7	13,3	5,3
46	1057	7,2	2,4	0,0	0,0	1,0	0,5	4,8	16,8	0,5
48	1167	2,5	0,4	0,0	0,0	1,1	1,4	0,0	20,2	1,8
50	1278	6,5	0,0	0,0	0,0	0,0	1,9	1,1	16,0	1,9
52	1389	7,4	0,0	0,0	0,0	1,9	1,0	1,3	11,6	2,6
54	1500	1,5	0,5	0,0	0,0	0,7	1,0	0,0	7,4	2,5
56	1588	7,3	0,0	0,0	0,0	2,4	0,4	2,0	16,3	0,8
58	1657	8,8	1,5	0,0	0,0	2,6	3,6	2,6	29,9	4,6
60	1725	11,4	1,6	0,0	0,0	1,6	0,8	2,4	23,6	0,0
62	1794	9,6	0,3	0,0	0,0	1,9	1,9	0,3	19,6	0,6
64	1862	8,0	0,3	0,0	0,0	1,7	2,1	0,0	20,6	2,8
66	1931	5,3	0,0	0,0	0,0	1,8	0,0	0,0	17,8	4,0
68	2002	5,3	0,4	0,0	0,0	1,4	0,7	0,0	11,1	0,5
70	2072	4,7	0,4	0,0	0,2	0,4	0,6	0,0	11,5	0,2
72	2142	15,6	2,0	0,0	0,7	2,6	1,3	0,0	18,9	0,0
74	2214	10,9	0,0	0,0	0,7	4,3	1,4	0,0	29,0	0,0
76	2284	22,7	0,0	0,0	1,3	0,6	1,3	0,0	30,9	4,4
78	2356	45,6	0,0	0,0	2,2	2,2	2,2	0,0	80,4	2,2
80	2429	8,0	0,0	0,0	0,0	0,9	2,7	0,0	55,1	0,9
82	2503	37,6	0,0	0,0	0,0	1,5	1,5	0,0	96,3	6,0
84	2580	20,3	0,0	0,0	1,5	0,0	1,5	0,0	71,5	0,0
86	2655	8,0	0,9	0,0	0,0	3,6	0,9	0,0	28,5	2,7

88	2731	20,3	0,0	0,0	1,5	0,0	1,5	0,0	71,5	0,0
92	2889	23,3	4,5	0,8	0,0	0,8	5,3	0,0	41,4	2,3
94	2969	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

Table 5. Platbos 1 non-land pollen and non-pollen palynomorph data as influx rates. Depth = cm; age = cal yrs BP; cype = Cyperaceae; myrit = Myriophyllum tetraporate; myrip = Myriophyllum polypantoporate; gune = Gunnera; mono = Monolete spore; tril = Trilete spore; sord = Sordariaceae; dama = Damaged grains; cnld = Concealed grains.

depth	age	micr	macr
0	-50	0,527	60,0
6	-16	0,715	44,0
14	26	0,627	54,0
20	58	0,797	76,0
26	91	0,569	35,0
28	132	3,023	186,0
30	177	0,425	27,4
32	284	1,030	63,4
34	395	0,153	9,4
36	505	0,494	30,4
38	615	0,713	43,8
40	726	0,635	39,0
42	836	0,337	25,9
46	1057	0,272	21,8
48	1167	0,181	18,9
50	1278	0,198	12,8
52	1389	0,312	19,2
54	1500	0,067	8,2
56	1588	0,190	22,7
58	1657	0,363	22,3
60	1725	0,324	26,9
62	1794	0,169	24,4
64	1862	0,342	37,9
66	1931	0,264	27,6
68	2002	0,300	37,9
70	2072	0,201	27,8
72	2142	0,381	32,8
74	2214	0,161	9,9
76	2284	0,411	25,3
78	2356	0,226	13,9
80	2429	0,018	1,7
82	2503	0,082	7,6

84	2580	0,116	16,0
86	2655	0,014	1,6
88	2731	0,058	8,0
92	2889	0,582	35,8
94	2969	n/a	n/a

Table 6. Platbos 1 charcoal data as influx rates. Depth = cm; age = cal yrs; micr = microcharcoal (<150um); macr = macrocharcoal (>150um).